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# PROBLEMS OF
# ANIMAL ECOLOGY

RESEARCH work on the effect of the environment upon animals is growing into an extensive science which presents a scattered literature dealing with experiments and observations on a number of different species. This book does good service in drawing together much of this work, especially that on insect populations, and presenting it in a convenient form as a series of essays on some of the growing points of ecological research. The effects of temperature on development, the length of life of animals in different conditions, age distribution of populations and the methods of studying it, fluctuations in populations, distribution of animal communities in different habitats, and the relation of ecology to problems of heredity and the origin of species, are all treated concisely and in an original and stimulating manner.

# PROBLEMS OF
# ANIMAL ECOLOGY

BY

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# PREFACE

THE present book deals with some problems of animal ecology which—owing to their intrinsic or their formal difficulties—have been neglected in experiment, observation, and analysis. It is the aim of this book to show the necessary trend for promoting solution by experiment and observation, to start again the analysis of problems which stick fast at a blind end.

The contrast between physiological and ecological longevity seems to be one of the best introductions to the problems of animal ecology. The correlations between longevity and life-intensity offer important suggestions from the borderland of physiology and ecology.

The ecological interpretation of the life-history has passed its primitive stages and is by now a valuable instrument of prognosis.

The analysis of population growth has suffered hitherto from the neglect of the early stages of development. The new aspects which a complete population-analysis offers are discussed by means of experimental data obtained for *Drosophila*.

The problem of the so-called biological equilibrium, attempted by three different schools of thought, is ripe for a synthesis which will do justice to all of them.

Animal communities are treated generally in the same sense which has been accepted by plant-sociology. The analysis shows that the presence of high integrations to super-organistic structures in animal communities has not so far been proven. They remain valuable statistical units for descriptive and classification purposes.

The interaction of environment and heredity within the organism as demonstrated by the phenomena of diapause, sex-determination, geographical variation, and adaptation, necessitates a close co-operation between genetical and ecological biology. It is rather improbable that any one of those branches can be understood alone, without realizing the background of the other.

The book is no easy reading. The necessary documentation is always appended in tables and in illustrations. These documents permit the reader to form an opinion of his own. Their selection was not at random, but rather careful and—it is hoped—without any bias. Omitting these documents, the reading would have become easy, but easy reading should be avoided in the present stage of animal ecology, where the formation of theories is so easy and the basis of facts so narrow. Most of the illustrations are originals prepared especially for this book with a view to filling blanks in the ecological literature.

Young as the science of animal ecology may still be, there is room for a quiet reconsideration of earlier interpretations and for new attempts at synthesis as well as analysis. Science is not only concerned with the accumulation of facts but also no less with their interpretation and co-ordination. It is the intention of the author to strengthen this trend in ecological thought.

The thanks of the author are due to Mr. C. Elton for many kind services rendered in connexion with the printing of the book, to Mr. J. Ford for improving the style, and to Mrs. H. Rubel for a great deal of technical help in preparing the manuscript. References to literature are indicated by ciphers, those to notes by small letters.

F. S. B.

*Jerusalem, 1938.*

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# I

# PHYSIOLOGICAL AND ECOLOGICAL LIFE-TABLES AND CONNECTED PROBLEMS (LIFE-INTENSITY, AGE-STRUCTURE OF ANIMAL POPULATIONS, RELATION BETWEEN THE ECOLOGICAL AGES)

## 1. PHYSIOLOGICAL LIFE-EXPECTATION

EVERY analysis of life-expectation begins with a study and definition of physiological longevity. Physiological longevity may be defined as that life duration which a healthy individual may expect to live under optimal environmental conditions until dying by senescence. Such an individual, having exhausted its inborn vital potentialities, dies because death is the end of every organized life.

Any individual out of an animal population bred under optimal conditions or under an optimal sequence of conditions (climate, food, density, parasites, diseases, episites, &c., and accidents excluded) and selected from a thoroughly healthy and genetically homogeneous stock will die a physiological death, conditioned only by senescence. Assuming that conditions are always optimal and that genetically the stock is healthy and homogeneous, an ideal curve of longevity, or death, must be expected. All individuals should survive until senescence and death set in, within a short period following a logistic decline. The main difference would be due to the different longevity of the sexes and to the minor individual differences which are always met with, even in a genetically very similar stock. Ecological conditions induce a heavy infant mortality and a permanent but lower mortality until senescence, when the last individuals die.

However, no animal lives throughout life under optimal conditions, and the physiological life-expectation is not verified in nature. Also, no two individuals of the same population live under exactly the same conditions during their life, and no two individuals of gamogenic origin are exactly alike in their hereditary constitution, inborn resistance, and vitality (a). Whatever is said here for individuals holds still more for populations of the same species.

Even in the absence of enemies and diseases, the following factors induce a deviation from the ideal death curve:

A. Genetic: different genetic constitution; not thoroughly healthy constitutions.

B. Ecological: deviation from optimal conditions during one, some, or all stages (climate, food, density, &c.).

This is the reason why even those laboratory breedings which approach the ideal death-curve closest show deviations from the beginning onward.

Our actual knowledge of physiological longevity is rather limited.[1] Flower[2] has compiled all observations available for vertebrates, including the experience gotten from zoological gardens. However, whereas there is some sense in studying the average longevity of birds and mammals in their natural habitat, and also the average longevity of long-lived poikilothermous animals like tortoises, crocodiles, lizards, fish, bee- or ant-queens, &c., under the same conditions, the conception of longevity loses any meaning as soon as we try to apply it to the smaller and shorter-lived poikilothermous animals.

But before discussing this complicated situation we must decide as to the limits of individual life. With regard to death, this is simple, and the physiological inquiry as to the exact moment of death is of little importance. It rarely happens that the experimenter or the observer is in doubt as to whether an animal is dead or not. And even should there arise difficulties, means are easily found to settle any doubts.

It is rather astonishing how little thought has been given to the beginning of individual life. In mammals, the moment of birth, in birds, reptiles, and fish the moment of hatching from the egg, has commonly been accepted as the beginning of life. With regard to insects and other invertebrates, all developmental stages, except the imago, have been compared with the embryological development in mammals, &c., and have therefore been excluded from any inquiry into longevity.[3] Any entomologist will regard this statement as absurd. The homologies and analogies of developmental

(a) See note a, p. 180.

stages, however, will always offer opportunity for alternative or varying interpretation. The only possible way of settling these sources of misunderstanding is the definition: *Longevity is measured as the period beginning with the egg-fertilization* (or with the beginning of cleavage in parthenogenetically developing animals, or with the beginning of increased cell-division in animals reproducing by budding) *and ending with the death of the individual.* This solution, besides guarding us from embarrassing puzzles, ends the unjustified exclusion of the embryonic period from the life-period. Physiological as well as ecological and hereditary factors influence this important stage, as well as later ones, and the environmental resistance of this stage is often much less than that of any later age.

## 2. LIFE-INTENSITY AND LONGEVITY

Speed of development, as well as adult longevity, depend on environmental factors, mainly temperature and air humidity. High temperature and optimal humidity shorten the life-span, low temperatures lengthen it. Theoretically, at the threshold of development, animals could be kept in 'cold-storage' for an indefinite period of time. Practically, they will die slowly after some (generally rather long) period has passed. Temperature (as well as other factors) is thus not only a factor affecting the quality of the environment, but it also influences the speed of life and life processes.

In principle it seems admissible that within certain temperature limits of tolerance, which are specifically different and sometimes even different with populations of the same species, life-intensity is more or less equal at all temperatures. This means that long-lived individuals display the same total activity at low temperatures, as measured by metabolic processes, &c., at their natural death as do the short-lived individuals at high temperatures, where intensity is much higher per unit of time.

Physiologists have promoted the theory that, within the same species, longevity—apart from genetic constitution—is inversely proportional to the intensity of life. This statement, first made in respect of mammals[4] (man excluded), maintained that they show the same total sum of basic metabolism after the completion of growth. It has not been confirmed by other students.[5]

| *Species* | *Longevity* | *Netto calories (Rubner)*[4] | *Brutto calories (Puetter)*[5] |
|---|---|---|---|
| Man | 60 years | 725,800 | 725,000 |
| Horse | 30 " | 163,900 | .. |
| Cattle | 26 " | 141,090 | 253,000 |
| Dog | 9 " | 164,000 | .. |
| Cat | 8 " | 223,000 | .. |
| Guinea-pig | 6 " | 265,000 | .. |
| Lion | 31 " | .. | 323,000 |
| Elephant | > 100 " | .. | > 1,660,000 |
| Camel | > 30 " | .. | > 1,210,000 |

With regard to poikilothermous animals, however, this rule seems to hold (within certain limits of temperature, &c., genetic constitution being equal).

Pearl[6] has given a stimulating demonstration, in this respect, on the growth and longevity of cantaloupe seedlings nourished only by the food contained in their cotyledons, showing inherited vitality. Putting the mean of the experiment at 100 per cent., the result was as follows:

| | *Seedlings which lived* | | |
|---|---|---|---|
| | *14* | *15* | *16 days* |
| | % | % | % |
| Total duration of life | 95 | 102 | 109 |
| $CO_2$ rate per day of growth during growth-period only | 104 | 102 | 81 |
| Dry matter metabolized | 105 | 100 | 87 |
| Water metabolized | 104 | 100 | 88 |

In *Drosophila* similar results have been obtained. In series of flies reared at 18° and 28° C. the following results were obtained as regards relative differences in size:

| *Character* | *Difference in size between 18° and 28° C. flies expressed as percentage of the size of 18° C. flies* | |
|---|---|---|
| | *Males* | *Females* |
| Femur length | 7·0 | 5·7 |
| Tibia " | 6·9 | 6·0 |
| Wing " | 13·4 | 10·0 |
| Wing breadth | 13·1 | 9·4 |
| Mean of four characters | 10·1 | 7·8 |

Similarly, differences occur in the longevity of flies bred at these temperatures:

| *Temperature during adult life* | *Difference in longevity between 18° and 28° C. flies expressed as percentage of the longevity of 18° C. flies* | |
|---|---|---|
| | *Males* | *Females* |
| 18° C. . . . | 19·5 | 7·6 |
| 25° C. . . . | 16·1 | 12·7 |
| 28° C. . . . | .. | 7·0 |
| Mean . . . | 17·8 | 10·2 |

'These results indicate, with a considerable degree of probability, that in these experiments the quantitative effects of temperature differences upon the biological processes concerned in growth are of approximately the same order of magnitude as the quantitative effects of temperature differences upon the biological processes concerned in the determination of duration of imaginal life. This is the kind of numerical result which would be expected on the rate of living theory of life duration, because in both cases the effect of increased temperature is to speed up the *rate* of the biological processes involved. In the 18° C. flies we have a *slow rate* of energy expenditure in growth and during imaginal life (flies very inactive), and we should therefore expect on the theory the lengthened duration of imaginal life which we observe. In the 28° C. flies there is a short developmental period and a consequent *rapid rate* of energy expenditure during growth and during imaginal life (flies very active). This leads to the expectation of a short duration of imaginal life, which is in fact observed.'[7]

In *Daphnia magna*[8] the product of heart-beats per second (life-average) and average longevity is constant for both sexes:

$$\text{♂}\ 4{\cdot}3 \text{ beats} \times 37{\cdot}8 \text{ days} = 161{\cdot}5$$
$$\text{♀}\ 3{\cdot}7 \text{ beats} \times 43{\cdot}8 \text{ days} = 162{\cdot}1$$

whereas the duration of life of females exceeds that of males by 14·6 per cent. Longevity as a function of metabolic rate is also in agreement with experiments on influence of temperature. The influence of temperature on the intensity of physiological processes is well known, but it seems that temperature plays no part in the coefficient of utilization of energy in the living system, nor in the coefficient of utilization of nutritive substances for growth. This has been shown for *Proteus vulgaris*,[9] for muscle activity,[10] for the amount of sugar used up to form 1 gramme of dry substance in *Aspergillus niger*, which is the same for different temperatures.[11] In tadpoles the amount of substance stored during growth, as compared with that of substance burnt, is practically independent of temperature:[12]

| | | | | |
|---|---|---|---|---|
| Temperature, °C. . . . . | 8 | 10 | 14 | 21 |
| Age at which gills disappear, days . | 30 | 22 | 20 | 8 |
| Coefficient of nitrogen utilization . | 0·75 | 0·73 | 0·75 | 0·75 |

The same is true for the gaseous metabolism of insect pupae. In *Tenebrio molitor*[13] the total quantity of $CO_2$ produced during the pupal stage was:

| | | | | | |
|---|---|---|---|---|---|
| Temperature, °C. . . | 18·8 | 20·9 | 23·7 | 27·3 | 32·3 |
| Litre $CO_2$ per kilo . . | 59·0 | 59·6 | 59·1 | 58·0 | 59·3 |

A surprising result was obtained by Parker.[14] In breeding *Melanoplus atlantis* at different temperatures, the total amount of food consumed (dry weight) by 10 nymphs was as follows:

| | | | | |
|---|---|---|---|---|
| Temperature, °C. . . | 22 | 27 | 32 | 37 |
| Duration of nymphal stage, days . . . . | 94 | 54 | 27 | 25 |
| Food consumed, milligrams | 4,079 | 4,311 | 4,098 | 3,988 |

With alternating changing temperatures as well, no significant difference was observed in the total amount of food consumed during the nymphal stage. Similar results were obtained on caterpillars of *Phlyctaenia ferrugalis*.[15]

The theory that rate of metabolism and longevity react inversely is greatly supported by the fact that insects, after having been treated with poisons or having been subjected to other unfavourable influences in sublethal dosages, show a shortness of life-duration parallel to the intensity of the treatment. Females of *Ephestia kühniella* show, after treatment with $CO_2$, at 17·5° C., shortening of adult life (see table opposite):[16]

These results are confirmed empirically and controlled by the parallel measurements of the hysteresis reaction.

Most interesting results are obtained from observations on field-bees. The worker-bee, after a constant development period of 21 days and more or less constant 10 days' service as both a nurse-bee and as house-bee, turns into a field-bee of varying longevity. Phillips,[17] the outstanding authority on bee life, concludes his observations:

| *Age at treatment in days* | *Exposure in seconds* | *How many days aged* | *Theoretical life-duration* |
|---|---|---|---|
| 11·5 | 0 | 0 | 23·0 |
| 11·0 | 5·5 | 0·5 | 22·5 |
| 10·0 | 15·3 | 1·5 | 21·5 |
| 9·0 | 25·0 | 2·5 | 20·5 |
| 8·0 | 34·5 | 3·5 | 19·5 |
| 7·0 | 44·5 | 4·5 | 18·5 |
| 6·0 | 64·0 | 5·5 | 17·5 |
| 5·0 | 63·8 | 6·5 | 16·5 |
| 4·0 | 73·5 | 7·5 | 15·5 |
| 3·0 | 83·0 | 8·5 | 14·5 |
| 2·0 | 94·0 | 9·5 | 13·5 |
| 1·0 | 108·0 | 10·5 | 12·5 |
| 0·6 | 126·0 | 10·9 | 12·1 |
| 0·525 | 150·0 | 10·975 | 12·025 |

> 'The worker bees, which develop from eggs identical with those from which queens issue, live 6–10 weeks in summer and possibly 6 months or longer in winter. Those which emerge in time to take part in the gathering of a heavy honey crop usually live about 6 weeks, but if no nectar is available, the length of life is extended. Those workers which emerge at the close of summer are the ones which must live until the following spring if the colony is to survive, for there is no rearing of brood in normal colonies in winter. It is obvious that the length of life is influenced to a marked degree by the amount of work which they are called upon to do. Similarly queens live longer if they are not compelled to lay such large numbers of eggs. If bees winter badly, so that they are compelled to produce much heat, they often die, in the spring, faster than they are replaced by oncoming bees, a condition known as spring dwindling. Not all bees die in summer within 6 weeks of their emergence, for if all brood rearing is prevented, it may happen that the last bee will not die for 4 months. *All these facts indicate that a bee is born with a definite amount of ability to do work and when its energy is expended the bee dies.* It must not be concluded that bees have no recuperative power, but it is obvious that their term of life is limited by the amount of work they do.'

This conception is confirmed quite independently by two other observations. Lundie[18] counted, by means of an electrical device, the number of bees leaving and returning to the hive during the season of activity. 3·16 per cent. of the bees did not return, i.e. died in the field. This would mean that one bee makes 31·65 trips before death overtakes it in the field. Whereas the number of deaths within the hive is rather limited, about 32 trips per worker-bee would be the average amount of work per field-bee. Bodenheimer and Ben-Nerya[19] obtained a similar result by dividing the total number of trips per annum through the total production of bees during the same period:

$$6{,}533{,}880 : 220{,}145 = 29{\cdot}68 \text{ trips per field-bee.}$$

The agreement between both results is rather close, especially if the difference in climate and methods is considered. The results confirm the theory that longevity of field-bees depends rather on the number of trips than on any other factor. The same is true of the total adult life. The amount of work done by the nurse- and house-bee is more or less constant during the active season. When no brood is to be nursed, the amount of energy normally spent on these activities is economized and—along with the stop of field trips in winter in colder climates—permits the survival of these bees throughout the interruption of the brood-rearing cycle.

All these facts tend to show that the life-span to be expected is determined by specific and individual constitution, a given constant, and by intensity of life as measured by metabolism and activity, a varying magnitude. The life of a fly living at 30° C. is shorter than that of one living at 20° C., but the life-intensity of both individuals is equal. And what is true of longevity is also true of adult life-span alone.

Finally, the temperature-sum rule is in itself a strong argument in this direction. This is not only correct for development, but also for partial physiological processes. Thus in fish the duration of the breeding season is inversely proportional to temperature.[20]

The temperature-sum rule states that the product of time and effective temperature (= environmental temperature—development threshold) is constant. The hyperbola constructed in this way agrees with empirical data on development from the specific development threshold to an upper zone, above which heat does not accelerate development but actually becomes injurious, inhibiting its speed and finally leading up to death.

It is possible to construct not one but three such hyperbolae: the first one (A) lasts from oviposition, which is very close to fertilization in insects, to first oviposition of the adults. The entire development and pre-oviposition periods are included in this period. Another hyperbola (C) may be constructed, based upon oviposition to average adult mortality. The difference between C and A gives the average adult longevity. From an epidemiological point of view, both of these hyperbolae are of little value. We may therefore construct an epidemiological average (B) at the period when half of the eggs of the hatching generation are laid.

We could base hyperbola C, as well, on the longest longevity at the corresponding temperature, and thus obtain the maximal life-span. One glance at such curves suffices to see that it is impossible to give absolute values for longevity of poikilothermous animals. Other conditions being constant, temperature is the dominating factor. However, quite a series of other factors, as population density, food-conditions, humidity, &c., interact in nature with temperature, not considering the constitutional intra- and inter-population differences.

The only way out is to put the maximal longevity (or the average longevity) at 100. Only in this way longevities at different temperatures, or at different habitats, may be compared. This necessity for comparison of different generations of poikilothermous animals or of corresponding generations in different habitats or countries on a common scale has been hitherto overlooked.

It must, however, be kept in mind that the entire conception of constant life-intensity is not a mathematical rule, even when neglecting the genetic background.

At high temperatures most insects of the same genetical stock are smaller (as indeed are mammals and birds) than at lower ones. Leslie Smith[21] has explained some of the reasons, and probably the decisive ones, for *Hyalopterus pruni*. The rate of feeding of this aphid was related to temperature, and it was found that for a given increase in temperature the rate of feeding did not increase as rapidly as the rate of reproduction. This results in the relative starvation of young born at higher temperatures. Likewise, the smaller summer eggs of *Aonidiella aurantii*[22] cannot be expected to grow to the same size as winter adults, at least not at the same total expense of energy. However, the relations between the percentage variations in morphological differences and longevity are closely parallel in *Drosophila*.[7]

Environmental changes, such as those of temperature, often lead to a physiological reconstruction of the organism concerned. Marine animals living in different latitudes often show a higher basic metabolism in the warmer climate.[23] Rabbits adapted to constant heat are found to lose, to a considerable degree,[24] their ability to produce heat and keep warm under chilling emergencies. Those adapted to a cooler environment are more able to meet chilling conditions by increased heat production, but succumb to excessive heat much more readily than do those adapted to constant warmth. A few hours' cooling counteracts the depressive effects of heat, and keeps the metabolism just as responsive to chilling as does a constantly cool environment. Animals living in a cold or changeable environment rapidly exhaust their glycogen supplies when chilled, while combustion is much slower in those from the hot room.[25]

It is therefore not surprising that the results obtained are not all concordant. The statement of Titschak[26] that the quantity of food eaten by the cloth-moth *Tineola biseliella* is much larger at 15° C. than at 30° C., but that the relative consumption of food (per unit weight) is much higher at 30° C. than at 15° C., needs further inquiry. Possibly one quality, e.g. water, was the limiting factor, and physiological food-utilization of the other substances of the food was incomplete.

However, the real explanation is given by Kozhantschikow.[27] In studying some physiological processes of *Blatta orientalis* he obtained the following zones (see table opposite):

He characterizes physiological optimal conditions as the temperature zone in which all physiological processes proceed with moderate and comfortable rhythm. The speed of processes is not maximal, but may be accelerated to a higher maximum (more than doubled). These rhythms lead to a moderate relative effect of the activity of the individual processes and to their maximal total effect. The maximum of any process cannot be considered as the optimum.

| *Process* | *Minimum* | *Maximum* | *Pessimum* |
|---|---|---|---|
| | °C. | °C. | °C. |
| Gaseous exchange | 0 | 40–45 | 45–55 |
| Irritability | 5–10 | 35–40 | 40–45 |
| Frequency of respiration | 10–15 | 40–45 | 45–55 |
| Heart-activity | 10–15 | 30–35 | 35–40 |
| Feeding | 10–15 | ? | 30–35 |

The main point is that each of the different physiological processes has a lower threshold, optimum, maximum, and upper limit of its own, and these different processes are co-ordinated to a total and more or less efficient rhythm within the organism. A change in environmental conditions induces not only a change in the single processes but makes a re-co-ordination necessary. As long as such new co-ordinates are not forced into too large deviations from the optimal co-ordination, the length-intensity rule seems to hold good.

## 3. ECOLOGICAL LIFE-EXPECTATION

It is extremely rare for optimal conditions, or a sequence of optimal conditions, to be maintained throughout the life of any individual in nature, and physiological death by senescence is rather a rare exception than the rule. Unfavourable environment, heterogeneous genetical composition, diseases, enemies, accidents, &c., kill individuals of every natural population by scores, mostly during the most sensitive stages of development, before they have grown adolescent or mature. And for the large majority of the relatively few individuals which survive the full period of sexual maturity, the post-reproductive period is much shortened. This actual life-history of a population or a generation is its ecological life-history.

Fig. 2, I A illustrates the actual difference in the physiological and ecological life-history in the case of the desert locust. In social animals (man, termites, ants, bees) the ecological mortality is often greatly reduced, and both curves differ only slightly. In some cases, as in that of the honey-bee, practically no mortality occurs before the bee has left the hive as field-bee. The analysis of the factors causing the difference between the curves of the physiological and the ecological life-tables is one of the main tasks of animal ecology.

A small series of life-tables based on breedings or, in the case of man, on comprehensive census work will be produced below. It should be kept in mind, however, that breedings, if carefully carried out, offer sub-optimal conditions to the animal, and are therefore apt to lower the death-rate by providing protection from enemies, diseases, and accidents, by providing suitable food, sufficient in quantity and quality, and by maintaining a comfortable temperature and humidity. We can, therefore, learn relatively little from these life-tables. But by varying certain factors separately, we may study the influence of the individual major factors on longevity.

We shall begin with Pearl's work on *Drosophila*, as it analyses the influence of a series of external factors on longevity (Fig. 1). First we compare the vitality of wild *Drosophila* and some mutants of the second chromosome, with characters which have never before been connected with other than morphological changes of minor importance.[27]

This result with mutants of a highly homozygotic strain of wild *Drosophila* gives a clear idea as to the amount of constitutional variation in longevity to be expected in any heterozygotic insect population. In different strains of wild *Drosophila* adult longevity at constant conditions varied from 26 to 54 days.[28, 29]

The influence of temperature[7] is illustrated by the following figures, representing adult longevity of *Drosophila* females, under different conditions:

| *Temperature during adult life* | *Mean duration of life of flies reared at* | |
|---|---|---|
| | *18° C.* | *28° C.* |
| 18° C. | 70·61 | 65·25 days |
| 25° C. | 40·96 | 35·75 ” |
| 28° C. | 30·67 | 28·52 ” |

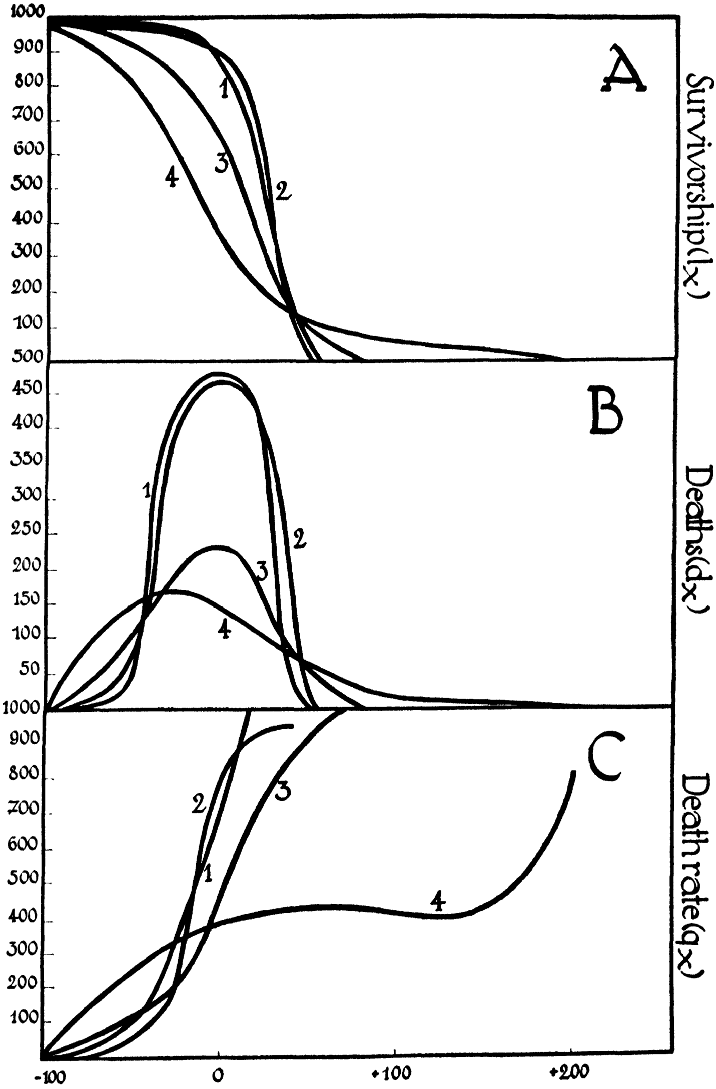


FIG. 1. Life-table curves of *Drosophila*. A. Survivorship (*lx*); B. Death curve (*dx*); C. Death rate (*qx*). The abscissa shows longevity, the mean longevity being assumed as O, all other ages being expressed as + or — percentage deviation from this mean. 1. Starved wild *Drosophila*; 2. Vestigial starved *Drosophila*; 3. Wild *Drosophila*; 4. Vestigial *Drosophila*. (After Pearl.)

TABLE 1. *Survivorship distribution of adults of wild* Drosophila *and single mutants at 25° C. (both sexes included, not weighed). (After Gonzalez.)*

| *Age in days* | *Number of survivors up to indicated age* | | | | | | |
|---|---|---|---|---|---|---|---|
| | *Wild* | *Quintuple* | *Black* | *Purple* | *Vestigial* | *Arc* | *Speck* |
| 1 | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 | 1,000 |
| 4 | 998 | 955 | 991 | 995 | 996 | 986 | 985 |
| 7 | 992 | 683 | 987 | 939 | 938 | 938 | 977 |
| 10 | 971 | 424 | 974 | 873 | 809 | 873 | 963 |
| 13 | 948 | 269 | 970 | 791 | 664 | 813 | 932 |
| 16 | 901 | 168 | 949 | 711 | 527 | 760 | 900 |
| 19 | 882 | 115 | 928 | 622 | 394 | 709 | 884 |
| 22 | 858 | 75 | 890 | 558 | 306 | 643 | 855 |
| 25 | 831 | 48 | 854 | 495 | 206 | 575 | 827 |
| 28 | 799 | 31 | 832 | 425 | 150 | 464 | 792 |
| 31 | 743 | 13 | 768 | 338 | 105 | 402 | 745 |
| 34 | 705 | 6 | 690 | 218 | 62 | 316 | 687 |
| 37 | 592 | 5 | 619 | 151 | 43 | 241 | 643 |
| 40 | 519 | 1 | 503 | 99 | 30 | 165 | 614 |
| 43 | 424 | .. | 420 | 67 | 8 | 107 | 544 |
| 46 | 342 | .. | 371 | 34 | 2 | 62 | 468 |
| 49 | 247 | .. | 293 | 20 | .. | 32 | 417 |
| 52 | 194 | .. | 241 | 7 | .. | 15 | 333 |
| 55 | 117 | .. | 196 | 3 | .. | 2 | 273 |
| 58 | 88 | .. | 119 | 1 | .. | 1 | 207 |
| 61 | 67 | .. | 65 | .. | .. | 1 | 149 |
| 64 | 45 | .. | 30 | .. | .. | .. | 102 |
| 67 | 32 | .. | 20 | .. | .. | .. | 50 |
| 70 | 20 | .. | 14 | .. | .. | .. | 24 |
| 73 | 8 | .. | 3 | .. | .. | .. | 15 |
| 76 | 1 | .. | 1 | .. | .. | .. | 2 |
| 79 | .. | .. | .. | .. | .. | .. | 2 |
| 82 | .. | .. | .. | .. | .. | .. | .. |

The influence of population density on longevity in *Drosophila* is to be gathered from the following compilation:[28]

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Initial density . | 2 | 4 | 6 | 8 | 10 | 15 | 25 | 35 | 55 | 75 | 95 | 105 | 125 | 150 | 200 | flies |
| Average density | 1·8 | 3·3 | 5·0 | 6·7 | 8·2 | 12·4 | 20·7 | 28·9 | 44·7 | 59·7 | 74·5 | 80·4 | 94·4 | 111·9 | 144·5 | „ |
| Mean longevity . | 27·3 | 29·3 | 34·5 | 34·2 | 36·2 | 37·9 | 37·5 | 39·4 | 40·0 | 32·3 | 27·2 | 24·2 | 19·6 | 16·2 | 11·9 | „ |

Fig. 1 illustrates the different important curves of the life-table for wild and vestigial *Drosophila* flies, starving and normal. It is clear that the mortality from egg to hatching of fly is excluded from these curves, which illustrate survivorship (*lx*) until the age referred to, the number of deaths (*dx*) occurring within each age-group of the population and death-rate (*qx*) of every age, provided the whole population is composed of that age-class only. For simplification's sake, all figures are referred to an initial population of 1,000 individuals born.

For further information on the ecological life-history of *Drosophila* the reader is referred to Chapter III.

Breedings of the desert locust (*Schistocerca gregaria*) in Egypt[29] served as a basis for calculating the mortality curve during summer. The breedings were performed in large cages at moderate to sub-optimal conditions. The biotic factors (enemies) were essentially excluded, but probably a few lizards entered the cage and fed on the locusts. The basic data were:

| Stage . . | egg | larva I | larva II | larva III | larva IV | larva V | Total |
|---|---|---|---|---|---|---|---|
| Duration in days | 27 | 8 | 9 | 11 | 8 | 12 | 75 |
| Percentage mortality . | 16·5 | 35·5 | 12·5 | 8·4 | 6·1 | 1·8 | 80·8 |

Sexual maturity was reached in June/July on the 155th day of life, i.e. the pre-oviposition period lasted 80 days. The hyperbolae are as follows:

| | *A* *pre-oviposition period* | *B* *at oviposition period* | *C* *A–B until average death* |
|---|---|---|---|
| Threshold (*c*), °C. | 17·4 | 17·4 | 17·4 |
| Thermal constant (*th.c.*), days-degrees | 978 | 1,322 | 1,930 |
| Duration in days at: 35° C. | 56 | 75 | 110 |
| 30 ,, | 77 | 104 | 153 |
| 25 ,, | 129 | 174 | 254 |
| 20 ,, | 376 | 508 | 743 |
| Average percentage of period | 50·5 | 17·5 | 32·0 |

Among the 19 adults, only 41·4 per cent. (=4·4) of the females and 50 per cent. (=4·5) of the males reach the beginning of sexual maturity. Supposing that each of those 4·4 females survives this period, which is rather improbable (only 1·8 females reaching the age of 200 days), the egg-production would be: for each female, 2·1 egg-pods (=114 eggs), i.e. 487 eggs total. Considering that actually only 300 eggs are laid, 200 eggs are still supernumerary under the conditions of this breeding. However, under natural conditions, mortality would have been much heavier. Parasites such as *Idia lunata* or *Chortophila cilicrura* and fungal diseases would have decimated the egg-stage; lizards, birds, small mammals the larval stage; larger birds and mammals (including man) the adult stage (Fig. 2, 1).

TABLE II. *Life-table of* Schistocerca gregaria (*bred in large outdoor cages, in the summer in Egypt*).[30]

| *Age in days* | *lx* | *dx* | *qx* | *Factors decimating the stage in nature* |
|---|---|---|---|---|
| 0 | 100·0 | 0·0 | 0·0 | Egg: Parasites: *Idia*, *Chortophila*, |
| 5 | 99·0 | 1·0 | 1·0 | &c. Fungous diseases |
| 15 | 94·0 | 5·0 | 5·1 | |
| 25 | 87·0 | 7·0 | 7·5 | |
| 35 | 61·5 | 25·5 | 29·3 | Larvae: Lizards and small mammals, |
| 45 | 34·5 | 27·0 | 43·9 | birds, man |
| 55 | 26·0 | 8·5 | 24·3 | |
| 65 | 21·5 | 4·5 | 17·3 | |
| 75 | 19·5 | 2·0 | 9·3 | |
| 85 | 19·5 | . . | . . | |
| 95 | 18·3 | 1·2 | 6·6 | |
| 105 | 16·0 | 2·3 | 12·6 | Birds and mammals |
| 115 | 13·8 | 2·2 | 13·7 | |
| 125 | 12·8 | 1·0 | 7·2 | |
| 135 | 12·2 | 0·6 | 4·7 | Man |
| 145 | 10·8 | 1·4 | 11·4 | |
| 155 | 9·1 | 1·7 | 15·7 | |
| 165 | 8·2 | 0·9 | 9·9 | |
| 175 | 7·3 | 0·9 | 11·0 | |
| 185 | 5·8 | 1·5 | 20·5 | |
| 195 | 3·5 | 2·3 | 39·6 | |
| 205 | 3·5 | . . | . . | |
| 215 | 1·6 | 1·9 | 54·3 | |
| 225 | 1·6 | . . | . . | |
| 235 | 1·6 | . . | . . | |
| 245 | 1·0 | 0·6 | 33·3 | |
| 255 | 0·6 | 0·4 | 40·0 | |
| 265 | 0·2 | 0·4 | 66·7 | |
| 275 | 0·0 | 0·2 | 100·0 | |

Wiesner and Sheard[31] analysed the longevity of white rats of the stock of the Wistar Institute with variable diet

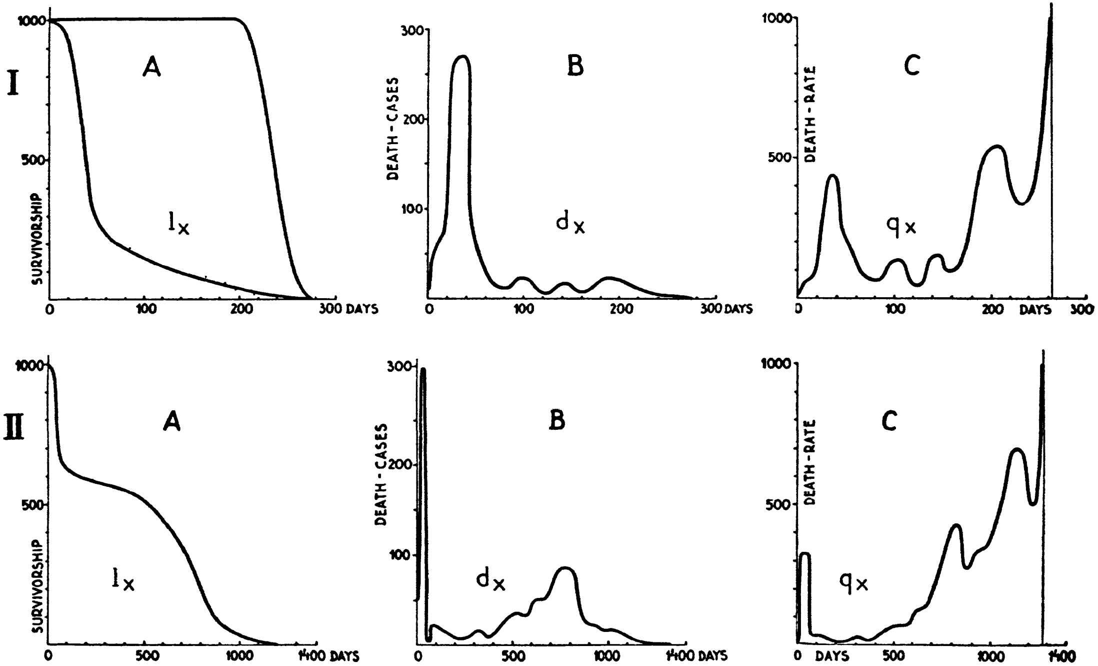


FIG. 2. I. Life-table curves of *Schistocerca gregaria* bred in summer in outdoor cages in Egypt. II. Life curves of white rats, bred under standard laboratory conditions. A. Survivorship (*lx*); B. Death-curve (*dx*); C. Death-rate (*qx*).

under standard, but not optimal, conditions. As only the weaned animals are included in the life-table, the following corrections should be made: in the following computation,

TABLE III. *Life-table of White Rats (bred under standard conditions).*[30]

| *Range* | *No. living at period* *lx* | *No. dying during period* *dx* | *No. dying in an equal-aged population during that period* *qx* |
|---|---|---|---|
| 0 | 100,000 | 5,000 | 5,000 |
| 23 | 95,000 | 31,023 | 32,660* |
| 53 | | | |
| 73 | 63,973 | 2,153 | 3,350 |
| 123 | 61,820 | 1,933 | 3,159 |
| 173 | 59,887 | 1,186 | 1,980 |
| 223 | 58,701 | 659 | 1,123 |
| 272 | 58,042 | 923 | 1,590 |
| 323 | 57,119 | 1,713 | 2,990 |
| 373 | 55,406 | 878 | 1,585 |
| 423 | 54,528 | 1,845 | 3,384 |
| 473 | 52,683 | 2,984 | 5,664 |
| 523 | 49,699 | 3,559 | 7,161 |
| 573 | 46,140 | 3,252 | 7,048 |
| 623 | 42,888 | 5,141 | 11,987 |
| 673 | 37,747 | 5,184 | 13,734 |
| 723 | 32,563 | 7,588 | 23,302 |
| 773 | 24,975 | 8,678 | 34,747 |
| 823 | 16,297 | 7,038 | 43,186 |
| 873 | 9,259 | 2,563 | 27,680 |
| 923 | 6,696 | 2,221 | 33,163 |
| 973 | 4,475 | 1,571 | 35,106 |
| 1,023 | 3,904 | 1,745 | 44,698 |
| 1,073 | 2,159 | 1,240 | 57,434 |
| 1,123 | 919 | 643 | 69,999 |
| 1,173 | 276 | 184 | 66,666 |
| 1,223 | 92 | 46 | 50,000 |
| 1,273 | 46 | 46 | 100,000 |
| 1,323 | 0 | 0 | 0 |

* All except 4 die between 23 and 52 days, 4 only at 53rd to 72nd day.

5 per cent. are assumed to die as foetuses during the embryonic development; 32·66 per cent. died, according to the observations of the above authors, due to neglect on the part

of the mother or to having been attacked by her during the first 30 days after birth. The embryonic period lasts 22 days (Fig. 2, 11).

In man, whose ecological mortality is greatly reduced by civilization, the comparison between the physiological and ecological life-tables is of lesser significance than in most other animals.[32, 33] Embryonic mortality is reduced to a very small number (artificial abortion excluded), as in all mammals, and the former high infant mortality is being gradually reduced. This is well expressed in Fig. 3.

In comparing now the theoretically possible types of life-curves of Pearl,[6] we realize that all these types are only realizations of ecological life-tables, which have no connexion with inborn physiological life-curves. The real type of inborn physiological longevity is represented by the starving *Drosophila* flies in Fig. 1, in which the previous development stages are added as a line running closely parallel to the 100 per cent. living line until the adult stage is reached. All these possible types of Pearl are realized in ecological life-tables, types D and C being the most common, type A being a rather unusual exception induced by catastrophic changes in the environment.

We finally shall define some conceptions connected with the study of longevity:

1. Life-span is the longest possible longevity of an individual within a species.
2. Physiological longevity is the average longevity of individuals of a population living under optimal conditions and of genetically homogeneous stock.
3. Ecological longevity is the empirical average longevity of the individuals of a population under given conditions.
4. The life-table reflects the course of mortality in a given population. Its more important columns are: $l$ = survivorship at a certain age; $d$ = death-cases occurring at each age-class; $q$ = death-rate at a given age-class, provided the entire population is composed of this age-class; $e$ = average life-expectance of an individual after having reached a given age.

The normal and usual conception of longevity is that called here ecological longevity.

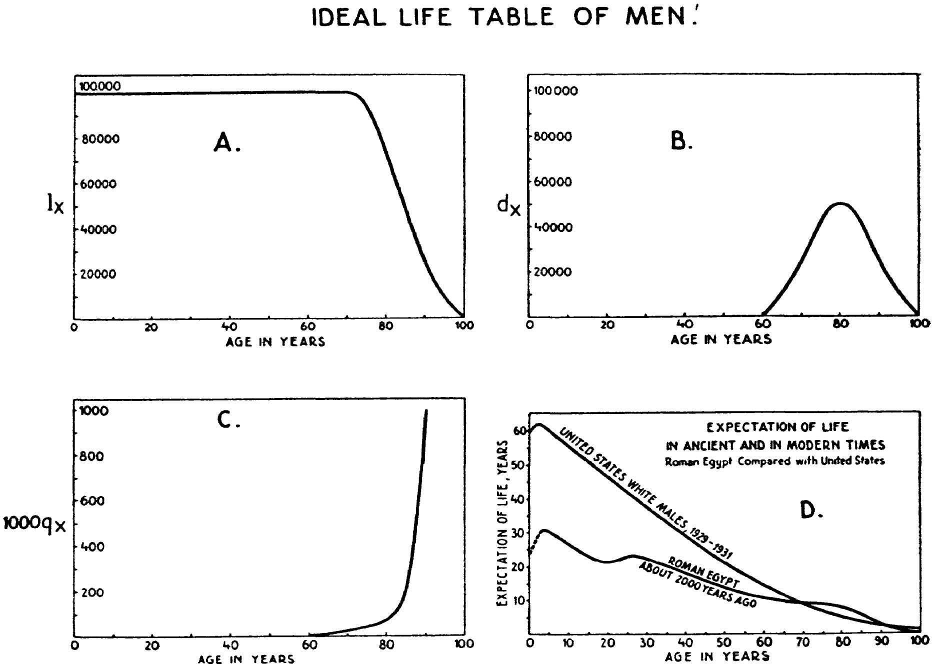


FIG. 3. Ideal (physiological) life-table curves of man and life-expectation in man. A, B, and C as in Fig. 2; D. Life-expectation in ancient and recent times. (D after Pearson.)

## 4. AGE-DISTRIBUTION IN ANIMAL POPULATIONS

A greatly neglected study in animal ecology is that of age-structure of populations. Such studies are available almost exclusively for man. And in man the age-structure is intimately connected with the state of growth of a human population.[34, 35] Fig. 4 illustrates the growing populations

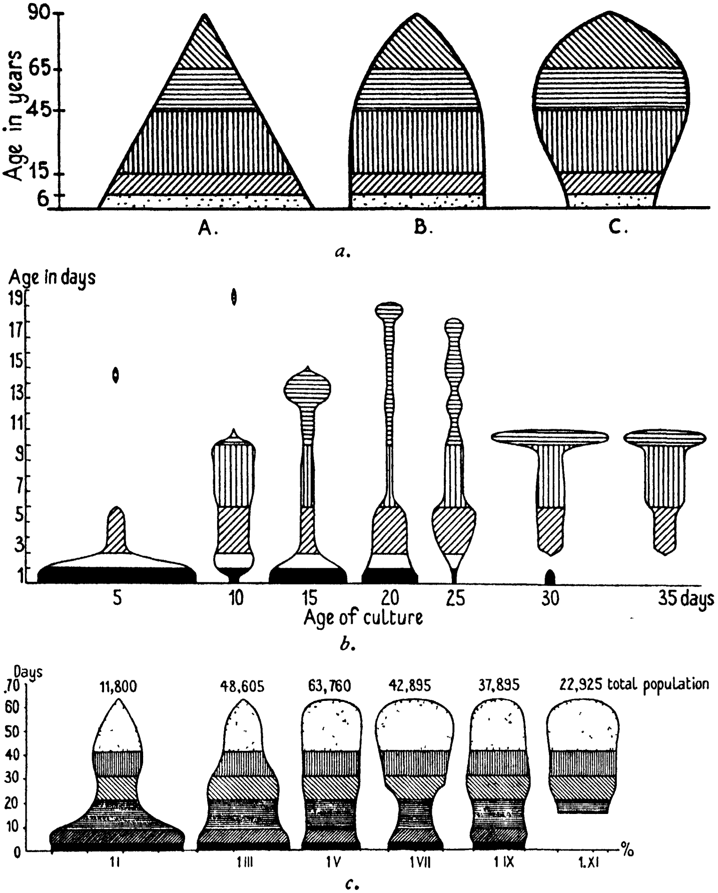


FIG. 4. Age-structure in changing populations (*a.* of man; *b.* of *Drosophila*; *c.* of honey-bee). A. Growing population; B. Stable population; C. Contracting population.

as a pyramid, the youngest age-classes being always more numerous than the preceding age-class. As soon as the population becomes stable, the pyramid changes into a bell, where all lower and middle age-classes are more or less equal, the higher ages diminishing slowly. In a dwindling population the birth basis is reduced successively and the higher ages form a disproportionate part of the total population (urn-shaped). This latter case is the common picture of larger town populations (migration excluded). It will be of interest to study animal populations in this respect.

The growth of animal populations within an empty space starts as unlimited growth until the environmental resistance begins to have an effect. And as we shall see, this influence of the environmental resistance begins at a rather early stage of population growth. A few types of population growth will now be analysed.

1. The most primitive type of population growth is that by simple division, met in most Protozoa and bacteria. It follows an exponential curve of the following formula:

$$P_n = P_1 \,.\, 2^n,$$

where $P$ = population, $n$ = number of divisions (= generations), $P_1$ = population at the beginning of the experiment, $P_n$ = population after $n$ divisions. In this case no age-distribution occurs, because the individuality of the generation ceases at the moment of the division, and the products of division become automatically the members of the following 'generation'.

Fig. 5, A illustrates this type of growth. None of the successive classes of the population live with those following, each class replacing the preceding one. However, no such curves of unlimited growth occur in nature. A real population growth of *Paramaecium multinucleata* has the following aspect (see top table, p. 24):[36]

The exponential growth is soon broken and changed into the general curve of organicistic growth, the logistic curve. This resistance is composed of two parts, working independently: destruction by enemies, diseases, accidents, &c., and inhibition of reproduction—in this case division. Highest population density creates an unfavourable environment and

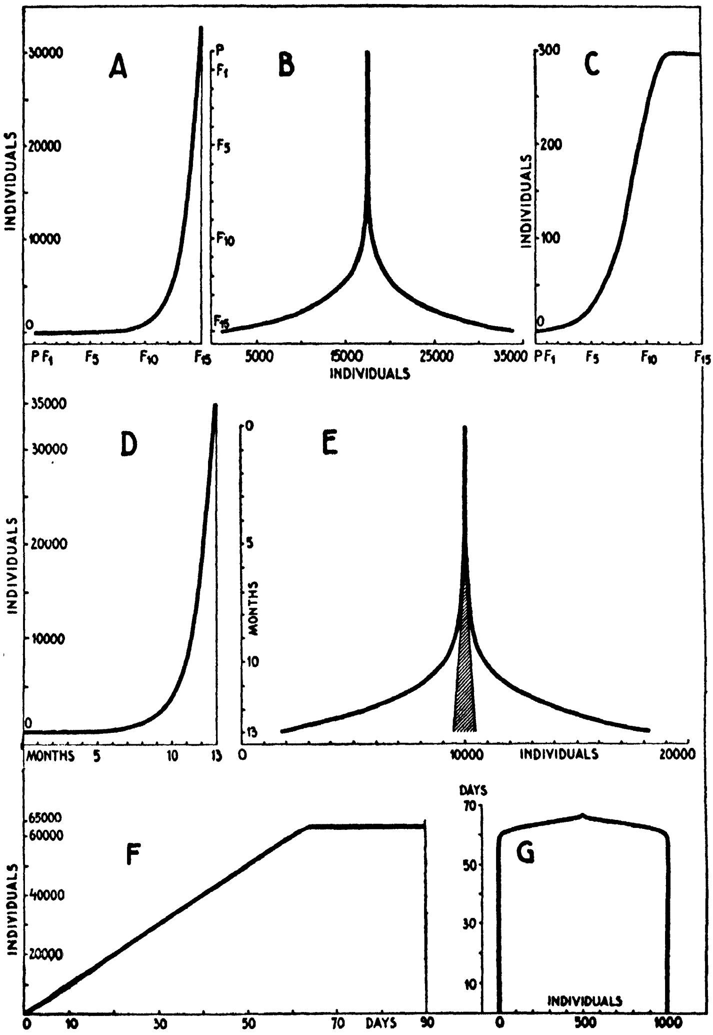


FIG. 5. Unlimited and limited growth and age-structure of animal populations. A to C, of Protozoa; D to E, of field-mice; F, G, of honey-bees.

A and D = exponential increase; B and E = age stratification of exponential populations (shaded area in E = actual age stratification); C = actual population growth of *Paramaecium*; F and G = ideal population growth and age stratification in honey-bees.

induces a new type of reproduction, i.e. conjugation. In our *Paramaecium* culture the latter factor alone worked. The following scheme may illustrate how destruction, as well as inhibition, induced up to a certain degree and increasing up to a certain point parallel to growing population density, will change the exponential into a logistic growth:

| *Age of culture in days* | *Mean number of Paramaecium per c.c.* | *Mean number of divisions per day* | *Approximate % of conjugants induced* |
|---|---|---|---|
| 0 | 1·4 | .. | .. |
| 1 | 5·1 | 1·85 | .. |
| 2 | 23·5 | 2·22 | .. |
| 3 | 108·8 | 2·21 | .. |
| 4 | 250·0 | 1·20 | 2 |
| 5 | 304·3 | 0·21 | 10 |
| 6 | 306·5 | 0·01 | 40 |
| 7 | 298·8 | —0·04 | 35 |
| 8 | 289·3 | —0·05 | 35 |
| 9 | 287·0 | —0·01 | 10 |
| 10 | 287·0 | 0·00 | 3 |
| 11 | 252·0 | —0·19 | 0·2 |
| 12 | 228·5 | —0·14 | .. |

| *Generation* | *Exponential growth by division* | *% destruction or inhibition per generation* | *Population growth after reduction as indicated in previous column* |
|---|---|---|---|
| P | 1 | .. | 1 |
| $F_1$ | 2 | .. | 2 |
| $F_2$ | 4 | .. | 4 |
| $F_3$ | 8 | .. | 8 |
| $F_4$ | 16 | 5 | 15·2 |
| $F_5$ | 32 | 10 | 27·4 |
| $F_6$ | 64 | 15 | 46·6 |
| $F_7$ | 128 | 20 | 74·4 |
| $F_8$ | 256 | 25 | 111·6 |
| $F_9$ | 512 | 30 | 178·6 |
| $F_{10}$ | 1,024 | 35 | 232·2 |
| $F_{11}$ | 2,048 | 40 | 278·6 |
| $F_{12}$ | 4,096 | 45 | 296·5 |
| $F_{13}$ | 8,192 | 50 | 296·5 |
| $F_{14}$ | 16,384 | 50 | 296·5 |
| $F_{15}$ | 32,768 | 50 | 296·5 |

The potential increase of any animal, the parents of which die when the young generations appear, is, in principle, similar to that of Protozoa. In many insects, tapeworms, fish, &c., we meet the same scheme, always inhibited in nature by intrinsic as well as extrinsic factors. In insect populations of overlapping generations the age-structure shows the same changes from pyramid over bell to urn in different growth-stages, as will be shown later in the essay on *Drosophila*.

Mammals, birds, and other long-lived animals show a somewhat different type of population growth. In voles, for example, many generations of the offspring reproduce freely simultaneously with their parents. In 3 years' lifetime one couple of *Microtus guentheri* may give rise to 22 generations ($F_1$–$F_{22}$) and itself gives birth to 31 litters. The total number of offspring of every generation produced from the beginning of the first year will be, at the end of this year:[37]

| *Age in months* | *Number of individuals* | *Total population in the month* |
|---|---|---|
| 12–13 | 2 | 2 |
| 11–12 | 6 | 8 |
| 10–11 | . . | 8 |
| 9–10 | 24 | 32 |
| 8–9 | 42 | 74 |
| 7–8 | 114 | 188 |
| 6–7 | 348 | 536 |
| 5–6 | 490 | 1,026 |
| 4–5 | 798 | 1,824 |
| 3–4 | 1,842 | 3,666 |
| 2–3 | 4,014 | 1,680 |
| 1–2 | 10,572 | 18,252 |
| 0–1 | 16,516 | 34,768 |

These figures are based on experimental breedings which yielded 6 young ones per litter, and births were observed at 35 days interval ($F_1$ after 25 days, first birth of neonate generation after 50 days).

The curves expressing age-distribution and potential growth require some comments. The age-distribution shows an absurdly large and ever rapidly extending basis. No such age-distribution is ever met with in nature. Even within a rapidly growing population, the part shaded in Fig. 5 E would be realized at the utmost. This means that heavy infant mortality must occur in nature. It is verified for voles, where the young ones are destroyed by enemies and unfavourable factors in a percentage much surpassing their numerical share.[38]

The same type holds for all mammals and birds, &c., with the only difference that the factor of increase is much lower and the rate of increase much slower. The elephant may serve as a theoretical example with 100 years longevity and 4 young ones on the average (m. = f.):

| Generation . . | P | $F_1$ | $F_2$ | $F_3$ | $F_4$ | $F_5$ | $F_6$ | $F_7$ | $F_8$ | $F_9$ | $F_{10}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Rise of population | 2 | 4 | 8 | 16 | 32 | 64 | 128 | 256 | 512 | 1,024 | 2,048 |

In the elephant, 10 generations extend over 500 years, whereas in voles over 16 months, in Protozoa over a day.

A particular type of restriction may be still discussed. In the beehive the number of reproducing individuals is reduced to one queen only. Similar cases occur in wasp, ant, and termite populations. The daily oviposition rate of such a queen depends highly upon environmental factors such as weather, amount of nectar available, status of population within the hive, &c. The author has shown that in bees where an annual seasonal trend in the hive-population can be observed the age-structure of the changing population has the same shape, from pyramid over bell to urn, as that of human populations.[19, 39]

Assuming that under constant sub-optimal conditions, which last for some time, the queen lays 1,000 eggs per day, the growth curve will differ greatly from the exponential one. The reason is, of course, the restriction in the number of reproducing individuals. The mortality in beehives at sub-optimal conditions seems to be negligible. Through the 21 days of development, the 10 days of nurse-bees, and the 10 days of house-bees, the population would show a daily increase of 1,000 eggs. The last 21(–24) days of the field-bee would show on the 62nd to 66th day the beginning and end of mortality. Fig. 5 F and G shows this type of increase and age-distribution. The formula for this type of growth would be as follows:

During the first 63 days of growth: $P_n = a.e$
After that period: $P_n = 63.e$,

where $a$ = age of population in days, $e$ = constant daily oviposition rate.

The age-distribution after the 63rd day is of the typical bell shape of a stagnant population.

The age-structure of a population serves, if the bionomic constants for the species are known, as an important indicator of the life-table of the population concerned.

### 5. RELATION BETWEEN THE THREE ECOLOGICAL AGES

From a physiological point of view the relative age of an organism may be divided into many categories, depending on growth of weight, size, linear growth, &c. The ecologist is interested mainly in age in connexion with reproduction. The life-span will thus be divided into development, lasting from fertilization of the egg until first birth; into the reproductive period, lasting throughout reproduction; into the post-reproductive period of senescence. Only for very few animals do we possess material based on sufficiently large-scale observations to enable us to get significant averages. A few examples of relative age are quoted below:

TABLE IV. *Relative duration of ecological ages in some animals*

| | *Development* | *Reproduction* | *Post-reproduction* | *Average longevity in days* |
|---|---|---|---|---|
| | % | % | % | |
| *Homo sapiens*, average | 22·1 | 51·7 | 26·2 | 17,430 |
| „ extreme | 12·9 | 45·2 | 41·9 | 19,254 |
| *Rattus norvegicus*, average | 24·8 | 20·6 | 54·6 | 1,104 |
| „ extreme | 11·7 | 37·6 | 50·7 | 1,374 |
| *Drosophila melanogaster* | 41·6 | 54·2 | 4·2 | |
| *Pieris brassicae* | 95·9 | 4·1 | .. | |
| *Schistocerca gregaria* | 50·5 | 17·5 | 32·0 | |
| *Ephemeridae* | 99·86 | 0·14 | .. | |
| *Panolis flammea* | 98·9 | 1·1 | .. | |
| *Periplaneta americana* | 69·9 | 27·2 | 2·8 | |
| *Tenebrionides mauretanicus* | 29·9 | 46·5 | 24·3 | |
| *Trogoderma granarium* | 83·0 | 11·9 | 5·1 | |

The main difference between mammals and insects in this group is the increased share of development and the reduced part of reproductive and post-reproductive period in the insects. This is conditioned mainly by the shift of the total feeding period into the larval stage (Ephemeridae), whereas in species with a long-lived adult stage (*Tenebrionides*) the share of each period resembles closely that of both mammals. The difference is therefore not of prime importance.

# II

# THE LIFE-HISTORY AND ITS ECOLOGICAL INTERPRETATION TO-DAY

ONE of the American pioneers in ecology once said that the life-history of the individual species will always remain the basis of animal ecology. This statement is no doubt true. The question, however, as to what should be understood by life-history has recently undergone many changes. It is not any longer restricted to the description of stages and of parasites and predators. The abundance of recent methodological achievements is large. Only a few of the more important implications will here be discussed.

Exact determination, description of all stages and ages, observations on their duration in the field as well as under experimental conditions in the laboratory, observations on reproduction and fertility on normal and occasional food (qualitatively and quantitatively, and especially on nutritional mortality), and statistical measurements of environmental resistance are still standard requirements and there is no need to dwell on them. We propose here to deal mainly with some problems of physical ecology.

## I. THE PHYSICAL ECOLOGY OF THE LIFE-CYCLE

The duration of the life-cycle depends on many environmental factors, of which the chief one is always temperature. Humidity, quantity, and quality of accessible food, &c., are other important factors, but for the normal life-cycle of most animals their importance is small as compared with that of temperature. Other factors, however, may need to be used for local corrections of the pure temperature dependency.

We do not intend here to take up again the discussion of the curve approaching nearest the experimental data of temperature, humidity, &c., dependency of development.[1, 2] For the intermediate zone, hyperbola and parabola, as well as catenary curve, are all in rather close agreement with the data. The inhibition of development above the point of shortest development must be found experimentally for the last two types of curves, whereas it may easily be entered as a correction into the hyperbola, wherever this upper zone is needed. The three distinct advantages of the equilateral hyperbola are:

1. The extremely simple way of computation, an important fact considering the mathematicophobia of most biologists.
2. The easy way of getting the basic data for calculation and of improving the curve by additional data.
3. Last, but not least, only the hyperbola furnishes us with the value for the lower development threshold, which value has proven to be of highest importance in ecological conceptions and calculations. This value is not obtained by any other formula.

The corrected temperature-sum rule is, within a certain vital range, certainly a very close description of the facts observed. Its exactitude and value should, however, not be exaggerated, as every mathematical approach in biology serves only as a short description of biological observations. Neither should the hyperbola be interpreted as the best physiological solution to the problem of temperature dependency. For ecological purposes, however, it has proven invaluable, not only because its immediate values are of greatest importance and interest, but also because many other applications of this simple formula may be advantageously made.

Some of these applications may briefly be mentioned:

1. The thermal constant is in certain cases the limiting factor in northern distribution. The area of *Gueriniella serratulae* is limited wherever the local annual sum of efficient temperature falls below the thermal constant.[3]

2. In certain species splitting into variations, or subspecies, has occurred in the zone in which the thermal sum divides the area of the species into areas with one or two generations per year or one generation in two years, as is the case within the 'Rassenkreis' of the pine shoot moth *Evetria buoliana*.[4]

3. The calculation of the theoretical local life-history by means of an hyperbola has proven of greatest value and

economy when correct, or, if incorrect, has stimulated research on other limiting factors.

4. The annual fluctuations of the sum of local effective temperatures above the thermal constant have proved of great use in explaining the local fluctuations of important insect pests.

5. The hyperbola permits application, not only for temperature-dependency of development, but also for activity, oviposition, &c.[7]

The first primitive form of the hyperbola as symbolic of the local life-cycle has undergone many improvements. Its final shape will be here exposed for the first time.

Whereas most of our earlier calculations for insects were based on the development only, ended by the appearance of the adult insect, we extend the development stage now until sexual maturity. And whereas in insects the fertilization of the eggs precedes oviposition, as a rule, only for a very short period, we may define the period of development as lasting from birth (oviposition of parents) to first oviposition. This does not interfere with the possibility of constructing, if desirable, separate hyperbolae for each of the development stages (e.g. egg, each larval and the pupal stage, pre-oviposition period). This hyperbola comprehends therefore the whole pre-reproductive period of the animal. But the animal does not die at the end of reproduction; a second hyperbola may be constructed for the average longevity of the individuals of any generation from birth to death. The construction of an intermediate hyperbola seems generally essential. For epidemiological purposes the average life-cycle of any generation is represented by a hyperbola which runs from birth to the end of the first half of normal oviposition (with regard to quantity of eggs, not to oviposition period). For other purposes it may be preferable to calculate the intermediate hyperbolae for the end of the reproductive period. In insects, however, the post-reproductive period of senescence is often negligibly short.

This triple band of hyperbolae permits the reconstruction of the local life-history with its overlapping of generations and its mixture of hibernating or aestivating generations, to a hitherto unknown degree of exactness and detail.

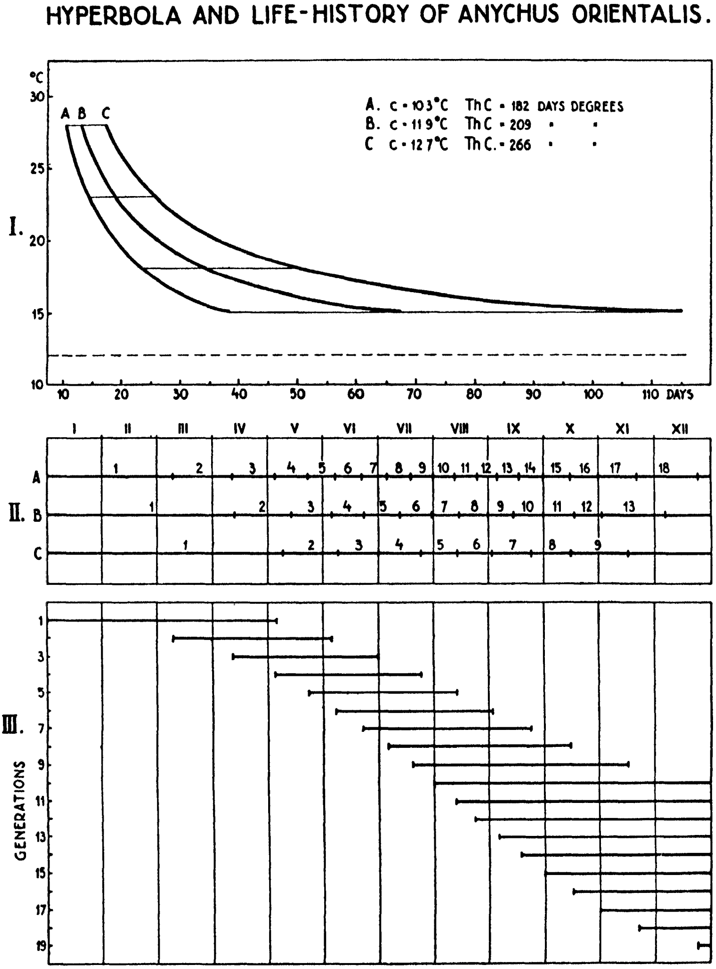


Fig. 6. Triple band of hyperbolae (I); local life-history (II); and succession of generations (III) at Tel Aviv for *Anychus orientalis*.

The representation of the life-history of the Oriental red spider *Anychus orientalis* may serve as an example (Fig. 6). The agreement of this calculated life-history with the actual one, which has been observed for some years by my associate

Klein,[8] is almost perfect. This agreement is the more significant as the relatively large number of annual generations would increase any important deviation enormously. The local life-history, as well as the local sequence of generations, have been worked out satisfactorily for quite a considerable number of citrus insects in Palestine.[10]

## 2. LIFE-CYCLES OF COCCINELLID BEETLES IN PALESTINE

Further improvements may be added for more complicated life-histories, as will be shown now for a family with especially complicated life-cycles, the Coccinellidae.

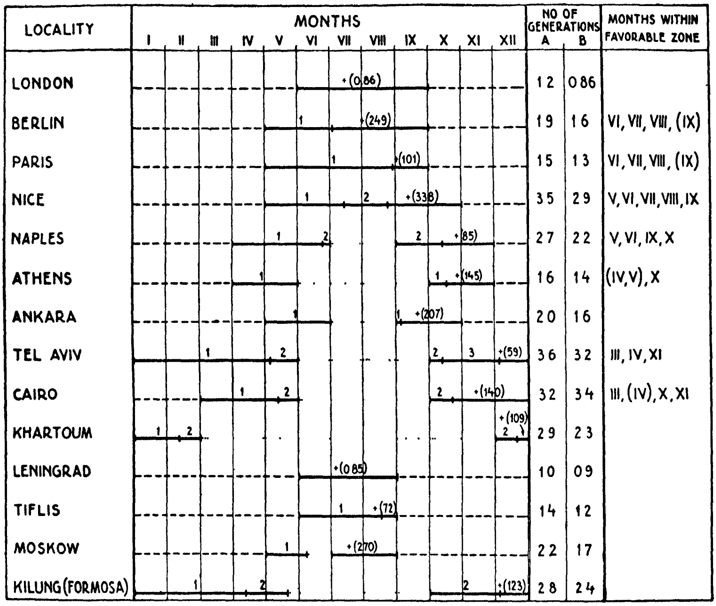
The simple life-cycle is often not realized, and it is desirable to introduce corrections within the simple distributional life-chart. The common 7-spotted ladybird, *Coccinella septempunctata*, may serve as an illustration of such corrections (Fig. 7).

Every interruption of development should be recognizable and may be represented by dots. Dots in winter mean either temperatures below the threshold of development or diapause. Aestivation may be designated by the same or by another mark.

In the northern zone, young adult beetles hibernate and begin to copulate and oviposit as soon as the spring temperatures rise above the threshold. Oviposition is somewhat protracted, especially at lower temperatures. The optimal temperature range for activity of adult beetles (including oviposition), as well as for development of immature stages, are temperatures between 15 and 17, and 20 and 22° C., and an humidity range from about 65 to 85 per cent. R.H. High humidity is decidedly unfavourable, and the same is true for much lower humidities.

There is no doubt that a consecutive series of months within this favourable climatic zone is more favourable than an interrupted one (e.g. compare Nice with Tel Aviv!). Double interruption, in winter and in summer, as in Athens, Ankara, &c., is likewise undesirable. The interruption in the summer is correlated with temperature. As soon as the average monthly temperature rises above about 23° C. oviposition, feeding, &c., stop and aestivation begins. No development takes place in this period. The combination of these double checks in activity and development leads to a surprising reduction in the number of annual generations. Whereas 9 (A) to 7 (B) annual generations would be computed for Tel Aviv without this correction, only two complete

PARTIAL WORLD CHART OF COCCINELLA SEPTEMPUNCTATA.



| LOCALITY | NO OF GENERATIONS A | NO OF GENERATIONS B | MONTHS WITHIN FAVORABLE ZONE |
|---|---|---|---|
| LONDON | 1 2 | 0 86 | |
| BERLIN | 1 9 | 1 6 | VI, VII, VIII, (IX) |
| PARIS | 1 5 | 1 3 | VI, VII, VIII, (IX) |
| NICE | 3 5 | 2 9 | V, VI, VII, VIII, IX |
| NAPLES | 2 7 | 2 2 | V, VI, IX, X |
| ATHENS | 1 6 | 1 4 | (IV, V), X |
| ANKARA | 2 0 | 1 6 | |
| TEL AVIV | 3 6 | 3 2 | III, IV, XI |
| CAIRO | 3 2 | 3 4 | III, (IV), X, XI |
| KHARTOUM | 2 9 | 2 3 | |
| LENINGRAD | 1 0 | 0 9 | |
| TIFLIS | 1 4 | 1 2 | |
| MOSKOW | 2 2 | 1 7 | |
| KILUNG (FORMOSA) | 2 8 | 2 4 | |

FIG. 7. Partial world chart of life-cycle of *Coccinella septempunctata*. Full line = development; dotted line = aestivation; interrupted line = hibernation.

generations and two incomplete ones are observed. The life-cycle may be summarized as follows:[9]

The hibernated beetles start oviposition in March. Their eggs form the first generation, the adults of which appear in April. A small number of the beetles of the first generation oviposit in May. Less than 1 per cent. of these eggs develop successfully into adults, and most of these beetles die before the beginning of oviposition. This II A generation is of no importance in the maintenance of the species. The great majority of the 1st generation, which has matured in April, aestivates. Oviposition and activity is resumed in the autumn (late September), a ndthe beetles die soon afterwards. The 2nd generation develops from their eggs in October. Some of these adults oviposit, forming a I a generation. A small proportion only of the eggs of this I a generation develops successfully into beetles which lay only very few eggs during the winter. These eggs do not develop. The few survivors participate in the formation of the normal 1st generation. The generation I a is therefore also of little importance in the maintenance of the species.

The brothers of those parents which did not oviposit in October hibernate. They are active, with interruptions, during the winter, especially on sunny days, and even oviposit occasionally. From the eggs of the hibernating 2nd generation, the 1st generation develops in March. We thus observe two annual generations in the coastal plain in spring and autumn which develop more or less sterile sidelines, one each in summer and winter.

Within the whole range of climates which we have analysed there are few tropical climates at higher altitudes which would permit more than 2–3 annual generations for *C. septempunctata*.

Similar seasonal limitations are illustrated in Fig. 8. However, these are winter interruptions only. The second column of Fig. 8 shows that there are other ways of passing unfavourable seasons. *Chilocorus bipustulatus* and *Cryptolaemus montrouzieri* undergo a very heavy summer mortality, which reaches up to almost 100 per cent. from June to August. Among the 4–5 generations, only a few adult beetles of 2 generations pass the summer, whereas the adults of 3 generations passing the winter undergo a much lower mortality.

Turning now to the local life-histories of some Coccinellid-beetles in Palestine, we find the most archaic type realized in *Lithophilus marginatus*.[10] This predator of *Icerya purchasi* has a prolonged adult diapause. The beetles hatch from May to September and remain sexually immature until the following spring. The total adult longevity was 523 days on the average, including 170 days oviposition, with 230 eggs per female. The maintenance of the species is thus well safeguarded. The poor season (autumn and winter) is passed by the immature adults, and adult longevity is long

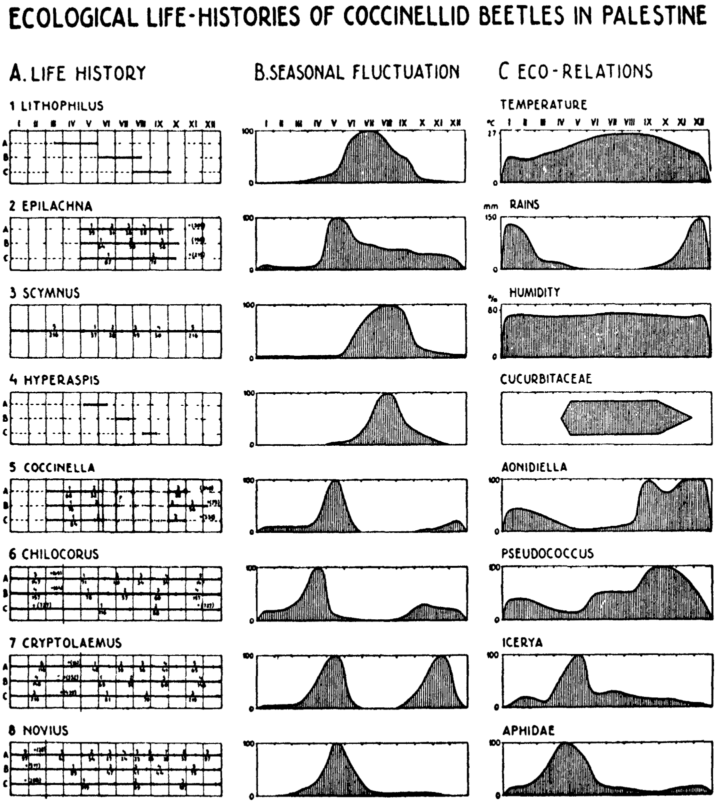


FIG. 8. Ecological life-histories of eight Coccinellid beetles in Tel Aviv (Palestine). A. Life-history as based on hyperbola B; B. Seasonal numerical fluctuation; C. Eco-relations—Physical ecology (temperature, precipitation, humidity) and numerical fluctuations of hosts (Aphidae, *Aonidiella aurantii*, *Pseudococcus citri*, *Icerya purchasi*, and cucurbitaceous plants).

enough to permit oviposition throughout spring and summer. The development of a fraction of the offspring is achieved even after a sequence of a few unfavourable months.

In *Epilachna chrysomelina*,[11] a pest of cucurbitaceous plants, there are six months of development and six months of hibernation. Whereas oviposition and other activities of the adult beetles stop at about 20° C., the threshold of development falls at 11·3° C. No development was observed from after the end of October to early May. From early May to the end of October, 5 generations were observed in breedings, 3–5 probably develop in nature, adults of the 3rd to 5th generation hibernating. The heliothermy of this species in the larval, as well as in the adult stage, tends to increase the utilization of the thermal possibilities. Two generations have been observed in South Africa by Gun. This agrees well with our formula:

| | *Annual generations* | | |
|---|---|---|---|
| | *Hyperbola A* | *Hyperbola B* | *Hyperbola C* |
| Capetown . . . | 1·3 | 0·7 | 0·5 |
| Wellington . . . | 2·0 | 1·1 | 0·8 |
| Simonstown . . | 2·7 | 1·5 | 1·0 |

In the subfamily Coccinellinae, *Hyperaspis polita*[10] approaches closest to the *Lithophilus* type. Oviposition is observed from May to August. The old beetles die in July–August, whereas the beetles of the current year hibernate. They do not seem to start oviposition in the same year until next May. Our observations on this point are not yet conclusive and are being continued. It seems doubtful, however, as to whether this early egg-laying has any importance, even if the first beetles of the year began oviposition in the same season.

In *Scymnus quadripunctatus* a continuous series of 5 annual generations is observed.[10] Beetles of the 4th, but mainly of the 5th generation, hibernate. This last generation develops in 217 days. Whereas winter is passed mainly in the adult stage, imaginal longevity, from spring to autumn, of the 1st to 4th generations, is rather short and rarely surpasses 4 to 6 weeks.

The rather complicated life-cycle of *Coccinella septempunctata* in Palestine has been discussed before. A partial world-chart of its life-history (hyperbola B) is illustrated by Fig. 7. The results of the calculation seem to agree well, indeed, with the known facts. We shall only mention by the way the fact that migration flights of these, as well as of other ladybirds, coinciding with the beginning or the end of the unfavourable season, begin, as in *Anopheles*, with a well-developed fat-body and end with the development of the ovaries. Fig. 7 explains the life-cycle of the common ladybird for the range of the Palaearctic sub-kingdom as well as for one locality at Formosa, the only region beyond the Palaearctic from which the species is reported. Further life-history studies of *C. septempunctata* would be extremely welcome from additional localities, but individual breedings throughout one year at least are required.

The armoured-scale ladybird, *Chilocorus bipustulatus*, has 4–5 successive annual generations.[12] The 1–2 summer-generations which follow the spring maximum have a much reduced egg-number and undergo a rather excessive mortality. The adults of 2–3 generations may survive the winter, but it is mainly those of the last pre-hibernal generation which do so. This behaviour is an approach to the complete summer diapause in *Coccinella*, but adult longevity is not yet extended sufficiently to safeguard the persistence of the species throughout the summer.

In *Cryptolaemus montrouzieri*,[13] which was introduced into Palestine for the purpose of controlling *Pseudococcus citri*, no acclimatization was achieved. The same is true for the species in Egypt, where acclimatization was attempted on a much larger scale (cf. [13]). Four to six annual generations undergo heavy climatic decimation in winter and especially in summer. Insufficient host density and lack of activity, even below the threshold of starvation at the elevated summer temperatures, bring about this result.

*Novius cardinalis*, the classical enemy of *Icerya purchasi*, is also, in its dynamics, the best adapted of all ladybirds studied. Five to nine generations follow each other without interruption, development extending to 3–4 months only, even in winter. Adults of 2–4 generations may pass the winter. Mortality is often high after heavy desert winds in the spring, whereas the summer heat is not very noxious. Host-density is a major factor determining the *Novius* populations.

The coincidence between all these life-histories and seasonal numerical fluctuation at Tel Aviv, physical factors (temperature, precipitations, humidity) and seasonal numerical host-fluctuation may be studied from Fig. 8.

We may conclude that this method of describing life-histories, if properly executed, shows a close correlation with the actual life-history. It illustrates all points of major importance for physical ecology, at least with regard to temperature. It illustrates well the often very complicated overlapping of generations in winter or at any other season. It has shown an easy and competent agreement with life-cycles calculated for other regions and localities. The method is easily executed and fulfils many desiderata unrealized hitherto.

## 3. APPLICATIONS OF THE CLIMOGRAPH

In animals which really have many annual generations—as is the case of *Anychus orientalis*—it will be possible to evaluate the optimal climatic conditions for the species by simultaneous observation of seasonal abundance. One must take care, however, to look less on the actual figures than on the quotient of increase. In a sequence of generations:

| Generation . . . | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| No. of individuals . . | 0·1 | 2 | 5 | 20 | 120 | 130 |
| Quotient of increase . | 20·0 | 2·5 | 4·0 | 6·0 | 1·09 | |

the transition from the 1st to the 2nd generation brings about the decisive increase. The absolute population abundance veils this fact very often. Anyhow, only the climate at the decisive periods of increase and not at the population peak should be regarded as optimal. Where only one to two annual generations occur, observations should be made for a series of years. But instead of the epidemiological approach we may choose also a zoogeographical analysis. In that case climographs of high medium and low abundance should be compared with regard to the common qualifications within each group. The aim of all such types of analysis is to be able always to circumscribe at least one climatically favourable zone. In the best case, we may be able to circumscribe an optimal, favourable, unfavourable, and impossible climatic zone.

Whenever this zonation is based on sufficiently large empirical data it becomes highly important for the understanding of seasonal fluctuation, local gradation, and geographical distribution. We shall give a few illustrations.

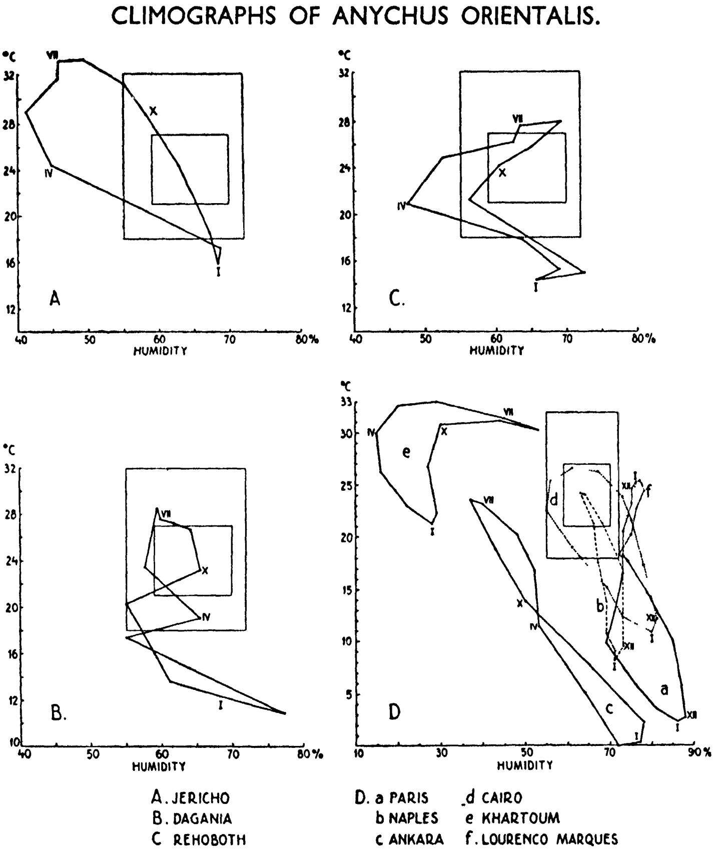


FIG. 9. Climographs of *Anychus orientalis*: A. at Jericho; B. at Dagania; C. at Rehoboth; D. at Paris, Naples, Ankara, Cairo, Khartoum, and Lourenco Marques.

Fig. 9 shows regional climographs of the various citrus-growing zones in Palestine with regard to the Oriental red spider *Anychus orientalis*. The inner rectangle designates the optimal zone, the outer rectangle (broken line) the limit of the favourable zone for this mite. It is now obvious why, at Jericho, the fluctuation peaks are in autumn and late winter, at Dagania (Lake Tiberias) from April until November, and in the coastal plain (Rehoboth) from June to October. This seasonal fluctuation is in total agreement with that actually observed.[8]

Diagram D in Fig. 9 explains clearly why 6 localities in 6 different zoogeographical regions do not offer an opportunity for any seasonal gradation or high population level of *A. orientalis*.

Whereas temperature always forms part of the climograph, it is not always clear whether humidity should be applied as precipitation or as relative humidity. This question may be settled only after knowing the biology of the species. Species, the eggs, larvae, and pupae of which dwell in the soil, as in the case of Noctuid moths, are subjected mainly to the influence of precipitation. Flies, &c., which are mainly subjected to air-humidity, on which depends their adult longevity, are most suitably analysed with regard to air-humidity.

## 4. THE EPIDEMIOLOGICAL BONITATION OF *Ceratitis capitata*.[15]

We shall now apply modern methods to the epidemiological bonitation of the Mediterranean fruit fly, *Ceratitis capitata*. We may define bonitation as the estimate of numerical development of an animal at any given locality or season, and its menace of danger if it is an agricultural or medical pest.

The three hyperbolae for *Ceratitis* are:

| | *A* | *B* | *C* |
|---|---|---|---|
| Threshold of development, °C. | 12·4 | 12·4 | 12·4 |
| Thermal constant, days-degrees | 339 | 745 | 1,218 |
| Duration in days of development | | | |
| at: 35° C. . . . . . | 15·3 | 33·0 | 53·9 |
| 30 ,, . . . . . | 19·3 | 42·5 | 69·2 |
| 25 ,, . . . . . | 26·7 | 59·1 | 96·7 |
| 20 ,, . . . . . | 44·6 | 98·0 | 160·3 |
| 15 ,, . . . . . | 130·4 | 286·5 | 468·5 |

Hyperbola *B* represents the epidemiological average of annual generations. But a few individual flies may survive for periods much longer than those given by hyperbola *C*, and those few survivors are of paramount importance for the maintenance of the species during unfavourable seasons, in which suitable hosts are rare or absent.

The physical zones of comfort of the species are:

| *Zone* | *Temperature range in °C.* | *Humidity range in % of R.H.* | *Bonitation index* |
|---|---|---|---|
| Optimal . . | 16–32 | 75–85 | 2 |
| Favourable . | 10–35 | 60–90 | 1 |
| Non-favourable . | 2–38 | 40–100 | 0 |
| Impossible . . | <2–40< | 40 | 0 |

In this way we obtain a reliable basis for climatic bonitation of *C. capitata*. The occurrence of 1–2 months, at least, within the impossible zone inhibits any permanent occurrence of the fly in the locality concerned, at least with regard to damage. In the non-favourable zone population density will remain very low. It will be higher in the favourable zone, and highest where favourable and optimal conditions exist for some consecutive months. In summing up the monthly values of the bonitation-index, we get the climatic local annual bonitation-value.

A series of additional corrections may be made to improve this bonitation:

1. Rainfall of more than 125 mm. combined with low temperatures (below 15° C.) is detrimental, especially to the pupae in the soil and to the adult flies. Such months should be corrected by deducting one unit from the sum of positive values. Prolonged lack of rains (irrigation lacking) is detrimental to the fly, directly by its influence on humidity and indirectly by its influence on vegetation.

2. The biological unit for measuring the importance of any factor to which the fly is exposed is the generation. The speed of its development depends mainly on temperature, and a special indicator consigns this speed of development in each month, as shown opposite.

3. Of greater importance, however, than both these factors are the host conditions. Abundant supply of favourable and suitable fruits for oviposition and development throughout the physically favourable season is optimal. Conditions

are less favourable when the hosts are present during a shorter period only, or when they are unsuitable, i.e. if eggs or maggots show a high nutritional mortality during development. Conditions grow uncomfortable when the sequence of more or less suitable fruits is interrupted for a more or less prolonged season and when hosts grow scarce in number. Wherever these conditions become even more extreme, the host-factor is very unfavourable to impossible. The bonitation concerning the host-factor should never be made for a whole country or region, but must be determined for each locality separately. Considering the importance of its host-factor and its dependency on two major components, we express it as a fraction.

|  | *1 generation in* | *Generation factor* |
|---|---|---|
| 10° C. . . | ∞ days | 0 |
| 10–15° C. . . | 50 „ (no oviposition) | 1 |
| 15–25 and 32° C. | 29–50 „ (including pre-oviposition period) | 2 |
| 25–32° C. . . | 18–29 „ „ „ | 3 |

$$\frac{\text{host suitability}}{\text{host abundance}}.$$

For the final damage bonitation we now proceed as follows: the climatic and generation-factors are multiplied by the sum of both host-factors, and eventually—before multiplication—the unfavourable rain-factor is deducted from the climatic factor. In the case when the host-factor is zero, it should be multiplied by the generation-factor only, only the climatic index being of importance.

We shall now proceed to give the actual bonitations. The climatic bonitation of the last 10 years for Tel Aviv is given:

|  | *Month* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Year* | i | ii | iii | iv | v | vi | vii | viii | ix | x | xi | xii | *In optimal* | *In favourable* | *In non-favourable* | *In impossible* | *Total* |
| 1927 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 9 | 3 | .. | .. | 21 |
| 1928 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 5 | 7 | .. | .. | 17 |
| 1929 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 5 | 7 | . | .. | 17 |
| 1930 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | .. | 12 | . | . | 12 |
| 1931 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 11 | .. | .. | 13 |
| 1932 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | . | 11 | 1 | .. | 11 |
| 1933 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 4 | 7 | 1 | .. | 15 |
| 1934 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | 1 | 1 | 6 | 6 | .. | .. | 18 |
| 1935 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 1 | 5 | 7 | .. | .. | 17 |
| 1936 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 1 | 4 | 8 |  | .. | 16 |

The climograph of *Ceratitis* at Tel Aviv (Fig. 10) confirms this important fluctuation, which for Jerusalem is still more important (minimum 1 to maximum 8), whereas in Jericho conditions are unfavourable (index: 0 to 2).

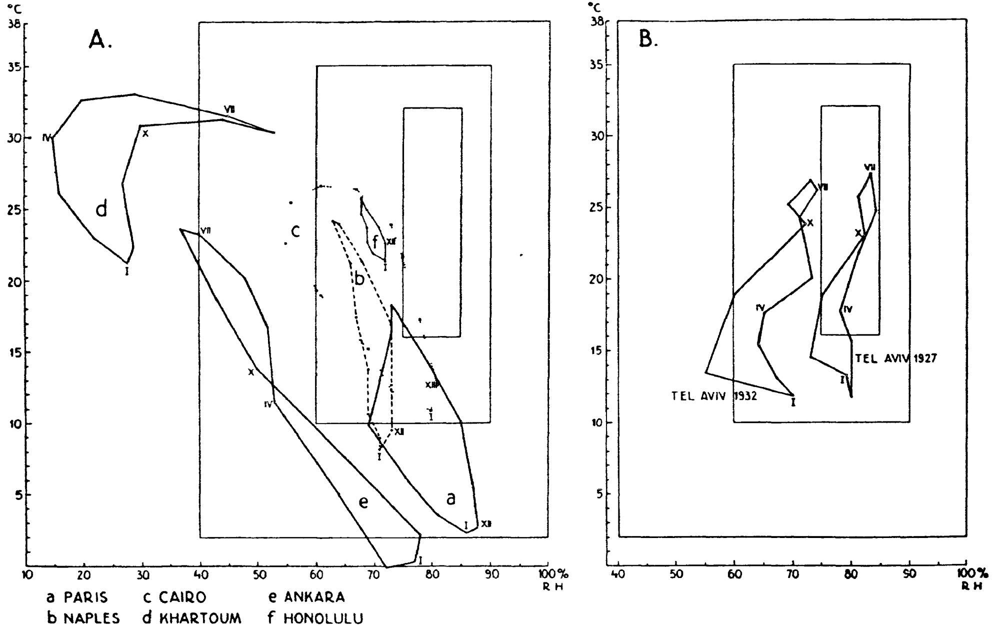
A complete bonitation of an orange grove in the neighbourhood of Tel Aviv in 1932 and 1934 respectively runs as follows:

*Complete* Ceratitis-*bonitation of an Orange Grove in the Neighbourhood of Tel Aviv in* 1932 *and* 1934

| | I | II | III | IV | V | VI | VII | VIII | IX | X | XI | XII | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *1932* | | | | | | | | | | | | | |
| Climate | 11·9 | 13·2 | 15·5 | 17·7 | 20·1 | 24·2 | 26·2 | 26·9 | 25·1 | 23·8 | 19·0 | 13·5 | °C |
| | 70 | 67 | 64 | 65 | 73 | 71 | 74 | 73 | 69 | 72 | 60 | 55 | % R H |
| | 131 | 96 | 8 | 3 | . . | | . . | . | 1 | 38 | 58 | 43 | mm. rains |
| Bonitation | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | Climatic index 11 |
| | −1 | . | . . | . | . | . | . . | | | . | . | . | Rain-factor |
| | 1 | 1 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 2 | 2 | 1 | Generation-factor |
| | 1/3 | 1/3 | 1/3 | 0 | 0 | 0 | 0 | 0 | 1/3 | 1/3 | 1/3 | 1/3 | Host-factor |
| Result | 4 | 4 | 8 | 1 | 1 | 1 | 1 | 1 | 12 | 8 | 8 | 0 | *49* |
| *1934* | | | | | | | | | | | | | |
| Climate | 12·8 | 11·7 | 16·3 | 18·5 | 21·6 | 24·9 | 26·7 | 27·1 | 25·7 | 23·2 | 19·2 | 14·4 | °C |
| | 76 | 79 | 71 | 80 | 80 | 77 | 79 | 79 | 74 | 75 | 73 | 80 | % R H |
| | 165 | 152 | 10 | 11 | 1 | | | | | 1 | 13 | 445 | mm rains |
| Bonitation | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | 1 | 1 | Climatic index · 18 |
| | −1 | −1 | | . | . | | . | . . | | | | −1 | Rain-factor |
| | 1 | 1 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 2 | 2 | 1 | Generation-factor |
| | 1/3 | 1/3 | 1/3 | 0 | 0 | 0 | 0 | 0 | 1/3 | 1/3 | 1/3 | 1/3 | Host-factor |
| Result | 4 | 4 | 8 | 2 | 2 | 2 | 2 | 2 | 12 | 16 | 8 | 4 | *66* |
| Changed host-factor | 1/3 | 1/3 | 1/3 | 2/2 | 2/2 | 2/2 | 2/2 | 2/2 | 1/3 | 1/3 | 1/3 | 1/3 | |
| Result · 1932 | 4 | 4 | 8 | 8 | 8 | 8 | 12 | 12 | 12 | 8 | 8 | 0 | 92 |
| Result · 1934 | 4 | 4 | 8 | 16 | 16 | 16 | 24 | 24 | 12 | 16 | 8 | 4 | *152* |

In Tel Aviv climatic conditions are favourable to optimal all the year round. In 1932 they were favourable, except for December. The rain-factor is only slightly unfavourable in January. No extreme drought decimates the adult fly population seriously. The generation-factor is very favourable from March to November. Host-sequence is fairly favourable, but is interrupted for 5 months. The main host is not very suitable. No high fly population can be present in September, but damage of late fruit may be expected from late March on.

In 1934 conditions are rather different. Whereas host-



CLIMOGRAPHS OF CERATITIS CAPITATA.

FIG. 10. Climographs of *Ceratitis capitata*; A. at Paris, Naples, Cairo, Khartoum, Ankara, and Honolulu; B. at Tel Aviv in 1927 and 1932.

and generation-factor remain constant, the rain-factor grows more unfavourable in December. The high precipitation in December has an effect only in the following year. Climatic conditions, however, are far more favourable. They are optimal from April to August, very close to optimal in September, and optimal again in October. No interruption occurs in December. The optimal climatic conditions in spring and summer permit the survival of a relatively high number of flies, which should be able and actually has been able to attack citrus fruits in September to a considerable extent. These conditions are improved, as far as the fly is concerned, by the fact that some other fruits are almost always available within the garden or in its neighbourhood throughout spring and summer. Apricots, prickly pear, figs, Lyctus, &c., are among the more common ones. The quantity and distance of these intermediate fruits determine the intensity of the attack on oranges in autumn. An uninterrupted sequence of suitable hosts, as has been alternatively calculated in the preceding table, would have resulted in serious damage in 1932, and in extremely serious damage in 1934.

We must content ourselves with regard to the value of the climatic bonitation factor in other localities within the area of distribution of *C. capitata*. The table on p. 47 serves as a starting-point in this discussion.

In the humid tropics favourable conditions for *Ceratitis* prevail everywhere in the lowlands, and at moderate elevations. This zone is probably the original home of the Mediterranean fruit-fly. In deserts (Saharo-Sindian and Northern Sudano-Deccanian regions) conditions are extremely unfavourable if special conditions do not maintain a high average air-humidity, as in Cairo. The same is true for steppe habitats (Irano-Turanian region). Mediterranean types of climate are rather suitable to the development of *Ceratitis*, as long as a relatively high humidity is maintained during the summer. The warmer parts of the region, especially, show high bonitation values, but lower ones than in the humid tropics. Winter rains and winter cold are rarely severe and long enough to exterminate the adult population.

The careful observer of the table on p. 47 will remark that the number of possible annual generations (hyperbola B) gives reliable results only in combination with the climatic bonitation. However, together they seem to give a fairly reliable picture of the climatic potential existing at any given locality for *C. capitata.*

*Climatic bonitation of some localities for* Ceratitis capitata

| *Locality* | *No. of possible generations* | | | *No. of months in zone* | | | | *No. of months below 12·4° C* | *Climatic bonitation* | *Region* |
|---|---|---|---|---|---|---|---|---|---|---|
| | *A* | *B* | *C* | *Opt* | *Fav* | *N fav* | *Imposs* | | | |
| Berlin | 1·8 | 1·1 | 1·0 | | 5 | 4 | 3 | 7 | 0 | Euro-Siberian |
| Paris | 1·6 | 1·1 | 0·9 | .. | 6 | 6 | . | 7 | 6 | ,, |
| Pinsk | 1·7 | 1·1 | 0·9 | .. | 5 | 2 | 5 | 7 | 0 | ,, |
| Ankara | 3·7 | 1·5 | 1·3 | | . | 9 | 3 | 6 | 0 | Irano-Turanian |
| Damascus | 6·3 | 3·2 | 2·2 | | 1 | 9 | 2 | 4 | 1 | |
| Nice | 3·3 | 1·7 | 1·4 | | 7 | 5 | | 6 | 7 | Mediterranean |
| Naples | 4·8 | 2·5 | 1·9 | | 9 | 3 | | 4 | 9 | ,, |
| Malaga | 6·6 | 3·5 | 2·5 | | 12 | . | | 1 | 12 | ,, |
| Tel Aviv | 8·2 | 4·2 | 2·8 | 2 | 10 | | . | | 14 | ,, |
| Cairo | 7·6 | 3·7 | 2·6 | 2 | 8 | 2 | . | 2 | 12 | Saharo-Sindian |
| Bagdad | 11·0 | 5·4 | 3·2 | . | 4 | 5 | 3 | 2 | 0 | ,, |
| Khartoum | 16·7 | 7·4 | 4·3 | .. | .. | 3 | 9 | .. | 0 | Sudano-Deccanian |
| Mongalla | 14·6 | 6·7 | 3·9 | 6 | 3 | 3 | | . | 15 | |
| Lourenco Marques | 10·2 | 4·9 | 3·1 | 7 | 5 | .. | | | 19 | Ethiopian Savanna |
| Salisbury | 6·6 | 3·5 | 2·5 | 4 | 4 | 4 | . | .. | 12 | S Africa |
| (Batavia) | 14·8 | 6·6 | | 12 | .. | . | | | 24 | Oriental Region |
| (Manila) | 15·1 | 4·7 | .. | 8 | 4 | | | | 20 | |
| Honolulu | 11·6 | 5·5 | 3·2 | | 12 | .. | . | | 12 | Hawaii |
| Tampa | 10·4 | 4·7 | 2·9 | 2 | 10 | | . | | 14 (*near* 17) | Florida |
| San Francisco | 1·6 | 0·7 | 0·5 | | 12 | | . | 4 | 12 | California |
| Los Angeles | 4·9 | 2·2 | 1·4 | | 9 | 3 | | | 9 | ,, |
| San Diego | 4·0 | 1·8 | 1·2 | 4 | 8 | . | .. | | 16 | ,, |
| Fresno | 6·1 | 2·7 | 1·6 | | 4 | 4 | 4 | 3 | 0 | ,, |

We shall just glance at the bonitation obtained for U.S.A. Hawaii, with a factor of 12 and 5·5 annual generations, as well as Tampa, in the centre of the now exterminated heavy infestation in Florida, with 4·7 generations and a factor of 14–17, offer decidedly optimal conditions throughout the year. At San Francisco all months are in the favourable zone, but fall below the development threshold in 4 of the temperatures and only 0·7 generations per annum may develop. During 4 months even optimal conditions prevail. In Los Angeles 9 months are in the favourable and 3, but these the less important winter months, are in the unfavourable zone, owing to low humidity. The latter, in addition, is probably efficiently counterbalanced by the not too heavy winter rains. The number of 2·2 annual generations approaches the danger-zone. Some damage could certainly be expected at San Diego as well as at Los Angeles.

In the dry interior of California the bonitation is very low. At Fresno the factor is depressed to zero owing to a sequence of 4 months of extremely low humidity.

Further co-operation is invited with regard to *C. capitata* in order to show the degree of agreement and to improve the bonitation by additional research.

### 5. SENSE ECOLOGY AND BEHAVIOUR

The living organism, its behaviour, and its reactions under natural conditions have been neglected all too long in research, whereas in reality this knowledge is just as indispensable as the knowledge of physical and biotic factors of the environment.[16] Eggs of the desert locust *Schistocerca gregaria* die in soil which is not thoroughly wet and aerated. It is of basic importance to know that the female locust never oviposits in dry soil.[17] An inherited chain of reflexes connects the exigencies of egg-development with the behaviour of the female rather closely. A large number of similar cases is known, especially in connexion with safeguarding the early development of the offspring. The colours to which the hawk-moth *Macroglossa stellatarum* is attracted change, in the gravid female, to that of chlorophyll, and this attraction, coupled with the smell of etheric oils of *Galium*, guarantees the proper oviposition and development of the caterpillars.[18]

Animals often migrate within their habitat into different strata or niches, or parts of the same host (interior or exterior, crown or root). It is of the utmost importance to verify in such cases whether these migrations are actively provoked by attraction to the new micro-habitat or whether they are simply the result of selection and survival.

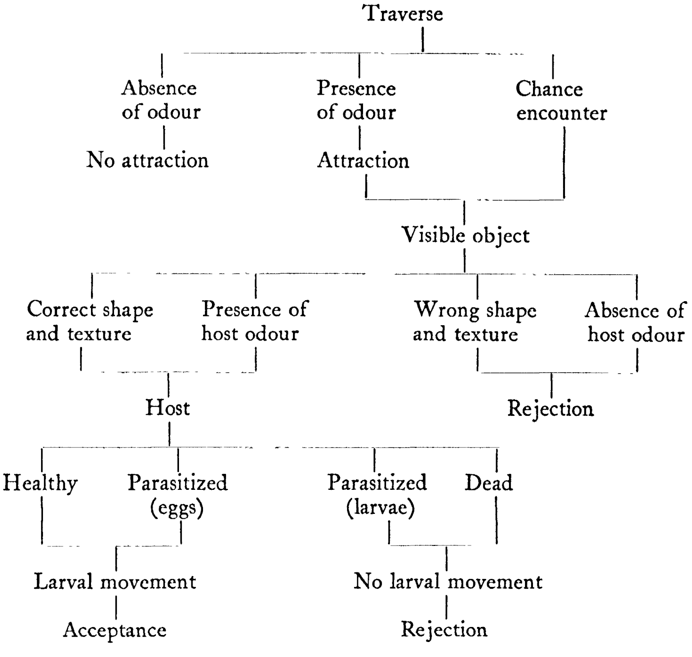
Taxisms are often influenced by environmental factors. Weber[19] has demonstrated in *Trialeurodes vapariorum* the following changes of behaviour in varying temperatures:

| Temperature, °C. | 10–15 | 15–20 | 20–25 | 25–30 | 30–35 | 35–40 | 40–45 |
|---|---|---|---|---|---|---|---|
| Phototaxis . . | 0 | + | + | + | ++ | ++ | − |
| Geotaxis . . | 0 | ++ | ++ | + | ± | − | − |

Success in finding food depends entirely upon the behaviour of the organism. It is necessary to know how far it may be able to direct itself actively towards its food, if at all, and if so, by which qualities of the food it is guided (chemical or optical sense, &c.).

Kennedy[20] has shown that the difference of one tactic reaction as compared in congeneric species (Dragonflies and Ephemerids) is sufficient to cause entrance into new niches or even new areas of distribution.

*Host selection by* Microplectron fuscipennis. *Tabular presentation of the course of events in the field.* (*After Ullyett.*)



It is deeply regrettable that the field opened by the ingenious work of v. Uexkuell[21] is so little worked on. Recently, work has been begun to explore the problem of recognition of the sex-partner, of the fellow or of the enemy. Quality after quality is deducted until the proper recognition as sex-partner, &c., ceases.

The parasite *Microplectron fuscipennis* is able to discriminate easily between true and false hosts even where the latter resemble the normal host in everything except the presence of the living larva within the cocoon.[22] Acceptance of a host seems to depend, to a large extent, upon the presence of larval movement.

Great efficiency is shown in discriminating between healthy material and hosts containing parasite larvae which are well grown. The presence of parasite eggs, on the other hand, does not deter females from ovipositing in the host. The reason for this difference is probably the larval movement, which is present in the latter and absent in the former case. There is thus a definite proportion of every host population which is not subject to random oviposition. A wholly mechanistic view of host selection is untenable, and the underlying basis of behaviour is of a psychological nature.

The presence or absence of social appetite[23] and its form and constancy, the form and constancy of sexual attraction, seasonal agglomerations or migrations, and their physiological and behaviour basis are of primary importance. The field and laboratory methods for studying those problems are rather inadequate to-day. It will be impossible, however, to work out standard methods, because every animal will require special methods to suit its special organization, requirements, and environment.

# III

# WHAT REALLY OCCURS IN THE *DROSOPHILA*-BOTTLE? A FURTHER APPROACH TO A COMPLETE POPULATION ANALYSIS

## I. *DROSOPHILA* AS MODEL IN POPULATION STUDIES

*DROSOPHILA* has been bred for the last two decades in a great number of biological laboratories, mainly for genetical purposes. It was R. Pearl[1] who laid the foundations of an experimental study of animal populations and their analysis by breedings of *Drosophila*. If one pair or a small population of *Drosophila* is introduced into milk bottles which are filled to a certain height with a standard larval food to which some yeast is added, the following facts are always observed: The growth of population begins at a slow rate, then becomes rapid and successively slackens its speed again until a saturation point is reached at which no further increase of population occurs. The growth follows a sigmoid curve, called the logistic curve, and is observed again and again wherever we have an opportunity to study the growth of animal populations, be it that of Protozoa in the test-tube or that of fish in ponds or that of human populations. If environmental conditions are constant and the experiments are performed with a genetically uniform stock, the course of the curve is very uniform in parallel breedings.

The mathematical characteristics of the logistic curve are a lower and upper asymptote and a turning-point. Its general formula is

$$y = \frac{k}{1 + e^{a+bx}},$$

where $y$ is the size of the population, $x$ the time (in age of population), $k$ the upper asymptote, and $a$ and $b$ constants.

Pearl counted the adult fly population and its growth only, since he regarded all previous stages, from egg to pupa, as comparable with the embryonic development of mammals or birds. He attempted to approach the physiological basis of the dynamics of the logistic growth-curve by a series of laborious as well as ingenious experiments. In each of these experiments all factors remained constant except one. This variable factor was, in one series, environmental (temperature, size or volume of milk bottle, composition of food, &c.), in another series genetical (wild strains and mutants of known genetical composition), while in a third series population density was the variable factor (longevity, fertility). It is to Pearl's permanent credit that he discovered the basic ecological importance of the density-factor in population-growth and in animal populations in general.

The results obtained with regard to longevity and to genetical composition of the fly population have been made use of in others of these essays. A few further results may be given here.

Wild *Drosophila* bred under various conditions gave the following results:[2]

| *Condition* | *Mean duration of life in days* | *No. of eggs per female-day* | *Total eggs per female* | *Wing length as indicator of body size* |
|---|---|---|---|---|
| | | | | *mm.* |
| Mean temperature | 27·7 | 29·3 | 812 | .. |
| Ditto, underfed | 39·1 | 9·9 | 387 | 2·81 |
| At 30° C. . . | 37·1 | 14·7 | 545 | 3·80 |
| In cold . . | 31·0 | 27·5 | 853 | 2·53 |

The difference of volume of the milk bottle influenced the environmental capacity (= upper asymptote) in the square of the volume of the universe in which it grows:

$$y = k \text{ (of smaller population)} \times \left(\frac{\text{large volume}}{\text{small volume}}\right)^2.$$

Each genetical strain has a different upper asymptote. Breedings in two different media showed a difference in $k$, which varied from 50 to 98 per cent.

## 2. BIOLOGICAL CONSTANTS OF THE PALESTINE STRAIN OF *Drosophila*

The great influence constitutional factors exercise on the events within the *Drosophila* bottle makes it advisable to illustrate the constants of physical ecology as well as some of the basic influences of density, as observed in our local strain, before proceeding with the analysis. We used a wild strain, the genetical constitution of which is entirely unknown, with which we have been experimenting for three consecutive years. The results seem consistent enough to justify the assumption that the strain is of sufficient genetical homogeneity to permit a population analysis. The volume of our milk bottles was 190 c.c., of which 50 c.c. were filled with agar 3 cm. high. The agar used was first composed as in Morgan's prescription (= normal banana-agar), whereas in the complete population count the synthetic medium of Pearl (S–101) was used. All population experiments were bred at 27° C.

The size and volume of the stages of *Drosophila* in young cultures were:

| | *Egg* | *Mature maggot* | *Pupa* |
|---|---|---|---|
| Size | 432 × 144 to 464 × 176 μ | 3,600 × 900 to 4,100 × 740 μ | 3,500 × 864 to 3,800 × 1,040 μ |
| Volume | 0·048 to 0·076 mm. | 0·386 to 0·6197 mm. | 1·414 to 2·155 mm. |

Development in relation to temperature was observed at 15, 20, 24, and 27° C., from hatching of adults to the hatching of the first individuals of the filial generation. The hyperbola of development (including the pre-oviposition period of the adult) shows the following constants:

Threshold of development (*c.*) = 10·1° C.
Thermal constant (*th.c.*) = 152.

The average development of different maggot stages was observed at 27° C. The average duration of the different stages was:

| *Stage* | *Egg* | *Larva* | *Pupa* | *Pre-oviposition period* | *Total* |
|---|---|---|---|---|---|
| Duration in hours | 25 | 94 | 97 | 24 | 240 |

of which 9 days fall into the development and 1 day into the pre-oviposition period.

These counts are utilized for the reduction of the observed number of individuals of every stage to the number produced. This correction factor is for the egg 1·04; maggot 3·93; pupa 4·04. The value observed must be divided by this correction factor.

The longevity of adult flies in our breedings was between

13 to 14 days in our population counts, 13·6 days in other series of low population density. Under the conditions of the experiment, the following three hyperbolae (Fig. 11, A) may be constructed:

| *Hyperbola:* | *A* (*development*) | *B* (*epidemiological average*) | *C* (*average total longevity*) |
|---|---|---|---|
| Threshold of development (*c.*), °C . | 10·1 | 10·1 | 10·1 |
| Thermal constant (*th.c.*), day-degrees | 169 | 267 | 382 |
| Duration in days at: | | | |
| 30° C . . . . . . | 8·5 | 13·4 | 19·2 |
| 27 " . . . . . . | 10·0 | 15·8 | 22·6 |
| 25 " . . . . . | 11·3 | 17·9 | 25·6 |
| 20 " . . . . . | 17·1 | 27·0 | 38·6 |
| 15 " . . . . . . | 34·5 | 54·5 | 78·0 |
| 13 " . . . . . . | 58·3 | 92·1 | 131·7 |
| Numbers of annual generations at 26° C . . . . . | 36·5 | 23·1 | 16·2 |

The sex-ratio of adult flies fluctuated between 55–60 per cent. females. We have here adopted the sex-ratio as 6 females to 4 males.

The influence of fly-density on fertility (Fig. 11, B) was studied in two series of experiments, in which, at 27° C., flies were transferred into new milk bottles for five successive days and the offspring bred:

| | | | | | | |
|---|---|---|---|---|---|---|
| Density of adult flies . . | 1 | 5 | 10 | 20 | 40 | pairs |
| Total egg-production . . | 409 | 656 | 553 | 599 | 1,031 | flies |
| Egg-production per female-day | 45·4 | 14·7 | 6·1 | 3·3 | 2·8 | " |

Normal fertility of *Drosophila* females (Fig. 11, C) was studied in milk bottles with the synthetic food-medium, two pairs of flies per bottle. The daily oviposition was:[3]

| *Day:* | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total oviposition . | 3 | 198 | 279 | 286 | 266 | 258 | 201 | 237 | 208 | 188 | 171 | 150 |
| No. of living females . | 10 | 10 | 10 | 10 | 10 | 9 | 9 | 8 | 8 | 8 | 8 | 7 |
| Eggs per female-day . | 0·3 | 198 | 279 | 276 | 276 | 288 | 223 | 296 | 260 | 235 | 213 | 214 |

| *Day:* | *13* | *14* | *15* | *16* | *17* | *18* | *19* | *20* | *21* | *22* | *23* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Total oviposition . | 113 | 86 | 73 | 46 | 16 | 22 | 21 | 21 | 3 | .. | .. |
| No. of living females . | 5 | 4 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | .. | .. |
| Eggs per female-day . | 226 | 215 | 365 | 230 | 8·0 | 22·0 | 21·0 | 21·0 | 3·0 | .. | .. |

The average longevity was 13·6 days, the average fertility 300·6 eggs per female. The values for the individual female-

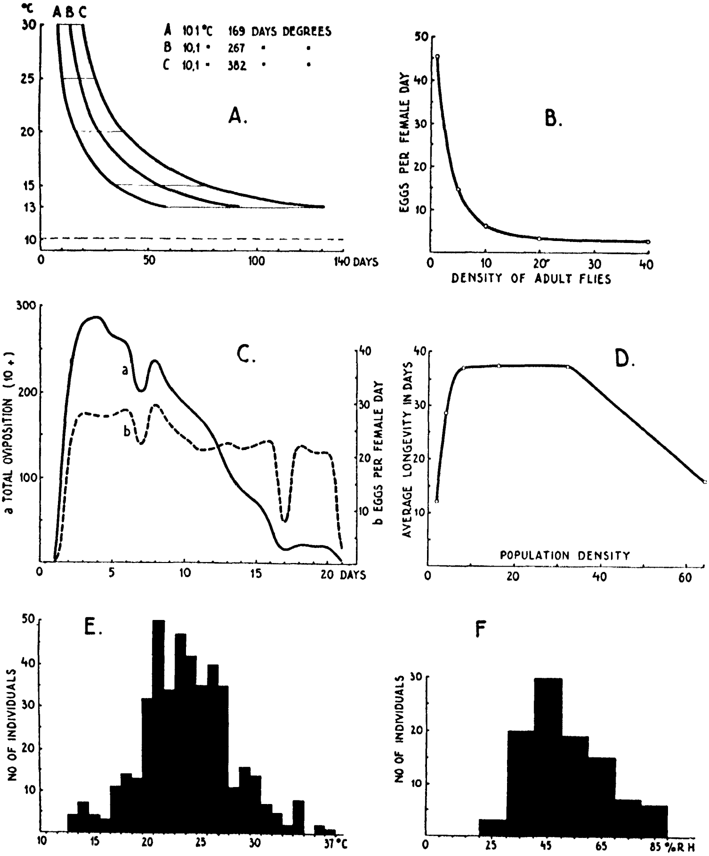


FIG. 11. Physical ecology of *Drosophila*. A. The three hyperbolae showing temperature-dependency of development (including pre-oviposition period), longevity and epidemiological average; B. Oviposition at different population densities; C. Total daily oviposition (*a*) and daily oviposition per female, (*b*) of 10 females; D. Adult longevity at different fly densities; E. Temperature-preference of adult *Drosophila*; F. Humidity preference of adult *Drosophila*.

day averages fluctuated from 14·3 to 29·0 eggs, for total oviposition from 136 to 520 eggs per female.

Conditions in our milk bottles must have been decidedly unfavourable for the adult flies. Longevity of adult flies is decidedly longer when no agar is in the bottles, but water with yeast only. At different densities of adult flies, the average longevity was, in the winter, at room temperature (Fig. 11, D):

| Population density | 2 | 4 | 8 | 16 | 32 | 64 pairs |
|---|---|---|---|---|---|---|
| Average longevity | 12·0 | 28·5 | 37·0 | 37·4 | 37·4 | 16·0 |

In another series, at 27° C., 14·6 days was the longest average longevity at a density of 32 pairs per bottle. Pearl's classical results are therewith fully confirmed: longevity shows a clean-cut density optimum, and is shorter when population density is lower or higher.

Some other constants of physical ecology include the preference temperature of the adults:[4]

| Temperature, °C. | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. of individuals | 4 | 7 | 4 | 3 | 11 | 14 | 13 | 32 | 50 | 34 | 47 | 42 | 35 |

| Temperature, °C. | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. of individuals | 40 | 35 | 11 | 16 | 14 | 7 | 5 | 2 | 8 | — | 2 | 1 |

The average of these 416 readings gives a preferendum of 24·1° C., 20 to 27° C. being the preferred zone (Fig. 11, E).

With regard to humidity preference the percentage-distribution in different zones of a humidity gradient was, among 534 readings:

| Humidity zone, per cent. R.H. | 20–30 | 30–40 | 40–50 | 50–60 | 60–70 | 70–80 | 80–90 |
|---|---|---|---|---|---|---|---|
| percentage of individuals | 3 | 20 | 30 | 19 | 15 | 7 | 6 |

The zone of 30 to 60 per cent. R.H. is the preference zone. This result is somehow surprising, as a higher preferendum would have been expected (Fig. 11, F).

The scale of activity in 104 individual experiments was:

| | °C. |
|---|---|
| 1. Upper limit of cold-torpor | 6·1 (5–7) |
| 2. Upper limit of unco-ordinated occasional movements of extremities only | 11·0 (10–12) |
| 3. Upper limit of slow crawling | 12·8 (12–14) |
| 4. Normal activity | 12·8–27·9 |
| 5. Lower limit of high activity | 27·9 (27–29) |
| 6. Lower limit of excited activity | 32·2 (27–34) |
| 7. Beginning of heat paralysis | 37·8 (34–39) |
| 8. Instantaneous heat-death | 39·6 (38–41) |

The normal range of activity extends from 12·8 to 27·9° C.; the high activity from 27·9 to 32·2° C. is certainly above the comfort-, but still below the danger-zone.

## 3. POPULATION GROWTH OF THE PALESTINE STRAIN OF *Drosophila*

We shall now proceed to describe the results of a series of experiments on the growth of *Drosophila* populations. All these breedings were made with Morgan's banana-agar as food-medium with the addition of yeast after the sterilization of the agar.

In the normal culture the number of adults begins to increase on the 10th day. The population maximum of 230 adult flies is reached on the 23rd day and is maintained with small fluctuations until the 31st day. The population then decreases until it is almost zero on the 50th day. The agar has dwindled away to a thin hard mass by this time and is entirely unfit as physical environment for the larvae. There is little doubt that if this food-medium could be kept fresh, a normal fluctuating population could be maintained for a long time.

Since Pearl compares the growth of human populations to that of *Drosophila*, it seemed to be of interest to see how artificial immigration of adult fly populations in the early part of population growth would influence the environmental capacity, i.e. the upper asymptote. Two series of observations were made, one with 6 flies introduced 5 times, from the 3rd to the 8th day, another with 30 flies introduced on the 3rd day of the culture. The results ($k = 253$, 246, and $230 = 243$) are identical with those of the normal individual cultures ($k = 234$, 234, and $283 = 250$), as was to be expected.

The formula of the logistic curve (as based on the average in No. 4) is for the normal cultures:

$$y = \frac{230}{1 + e^{1\ 9299 + 0\ 1702x}}.$$

Another series of breedings was arranged in order to study the influence of a different environment. They were performed in cylindrical tubes 5·5 cm. in diameter. The arrangement was as follows:

| *Series:* | *1* | *2* | *3* |
|---|---|---|---|
| Volume of agar, c.c. | 26·4 | 26·4 | 52·8 |
| Volume of air space, c.c. | 149·6 | 74·8 | 74·8 |
| Maximum no. of flies | 206 | 205 | 205 |

Despite the considerable difference in the volume of larval or adult environment, the vital capacity was identical in all series. (See note b, p. 180.)

A similar series was bred in Erlenmeyer flasks, which unfortunately did not yield clean-cut results. The process of taking out the flies daily for the counts caused the agar to become loose at an early age. The importance of the results should therefore not be overestimated. The comparison of the results with those to be expected from Pearl's volume-rule shows (Series 4 was destroyed as the agar became loose very prematurely):

| *Series:* | *1* | *2* | *3* | *4* |
|---|---|---|---|---|
| Volume of agar, c.c. | 85 | 122 | 255 | 350 |
| Volume of air space, c.c. | 250 | 320 | 665 | 1,650 |
| Maximal no. of adults | 218 | 218 | 443 | (525) |
| Ratio to air space of Series 1 | 1·00 | 1·28 | 2·66 | 6·60 |
| Ratio to flies of Series 1 | 1·00 | 1·00 | 2·03 | (2·41) |
| Calculated from volume rule | 218 | 358 | 944 | 1,439 |

The results of both these series, inconclusive as they may be, should stimulate further research on the influence of change of measurable larval as well as adult environment on the population capacity.

## 4. THE TOTAL POPULATION COUNT IN THE *Drosophila* BOTTLE AND ITS RESULTS

The analytical study of the dynamics of bee populations made it clear to the author that no dynamic analysis of population trends can be attempted without counting *all* stages of the species concerned. We have criticized before, from another point of view, the omission of any age from general life-tables or other statistical population census. It

# TABLE I. *Population growth of the Palestine strain of* Drosophila (*each series represents an average of 3–4 breedings*)

| | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 |
| 2 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 4 |
| 3 | 4 | 4 | 4 | 4 | *10* | *34* | 4 | 4 | 4 | 4 | 4 | 4 | 4 |
| 4 | 4 | 4 | 4 | 4 | *16* | 34 | 4 | 4 | 4 | 4 | 4 | 4 | 4 |
| 5 | 4 | 4 | 4 | 4 | *22* | 34 | 4 | 4 | 4 | 4 | 4 | 4 | 4 |
| 6 | 4 | 4 | 4 | 4 | *28* | 34 | 4 | 4 | 4 | 4 | 4 | 4 | 4 |
| 7 | 4 | 4 | 4 | 4 | *34* | 34 | 4 | 4 | 4 | 4 | 4 | 4 | 4 |
| 8 | 4 | 4 | 4 | 4 | 34 | 34 | 4 | 4 | 4 | 4 | 4 | 4 | 4 |
| 9 | 4 | 4 | 4 | 4 | 34 | 34 | 4 | 4 | 4 | 4 | 4 | 4 | 4 |
| 10 | 14 | 23 | 34 | 24 | 34 | 52 | 4 | 4 | 4 | 6 | 7 | 6 | 6 |
| 11 | | | . | .. | 81 | | 54 | 104 | 73 | 31 | 39 | 28 | 20 |
| 12 | 110 | 106 | 118 | 111 | | 100 | 120 | 193 | 134 | 69 | 81 | .. | 44 |
| 13 | 148 | 133 | 176 | 152 | 126 | 134 | 190 | *205* | 160 | 84 | 102 | 132 | 82 |
| 14 | 166 | 152 | 183 | 167 | 111 | 145 | *206* | 203 | 165 | 125 | 176 | 236 | . |
| 15 | 176 | 167 | 225 | 189 | 161 | 149 | 198 | 162 | 154 | *146* | *217* | 292 | 131 |
| 16 | 189 | 169 | 205 | 188 | 158 | 173 | 120 | 203 | 160 | 139 | 190 | 307 | 149 |
| 17 | 188 | *234* | 174 | 199 | 181 | 193 | 139 | 101 | *189* | 109 | 167 | 390 | 110 |
| 18 | 217 | 181 | *235* | 211 | 184 | 209 | 109 | 54 | 139 | 122 | 117 | 340 | 36 |
| 19 | 204 | 185 | 230 | 206 | 195 | 203 | 66 | 64 | 129 | 94 | 84 | 44 | 5 |
| 20 | 232 | 180 | 235 | 216 | 184 | 209 | 62 | 56 | 123 | 111 | 108 | *443* | 10 |
| 21 | *234* | 193 | 243 | 223 | 204 | 232 | 50 | 85 | 145 | 112 | 120 | 354 | . |
| 22 | 226 | 189 | 254 | 223 | 201 | 231 | 30 | 99 | 115 | 176 | 182 | | 215 |
| 23 | 209 | 204 | 278 | *230* | 211 | 244 | 45 | 83 | 141 | 179 | 212 | 368 | *525* |
| 24 | 199 | 186 | 208 | 198 | 222 | 244 | | . | | *218* | *218* | 308 | |
| 25 | 178 | 211 | 265 | 218 | 214 | *246* | 66 | 118 | *205* | 184 | 152 | 259 | *a* |
| 26 | 177 | 191 | 266 | 210 | *253* | 236 | 62 | 88 | 198 | 125 | 117 | 320 | *g* |
| 27 | 178 | 202 | 253 | 211 | 248 | 232 | 85 | 105 | 172 | .. | | 280 | *a* |
| 28 | 179 | 202 | *283* | 221 | 239 | 197 | 101 | 113 | 128 | 55 | 96 | 230 | *r* |
| 29 | 207 | 200 | 234 | 214 | 224 | 188 | 107 | 86 | 86 | 32 | 54 | 228 | |
| 30 | 224 | 182 | 235 | 214 | 224 | 176 | 91 | 77 | 83 | 91 | 65 | 226 | *l* |
| 31 | 232 | 201 | 230 | *221* | 214 | 183 | | | | 30 | 51 | 200 | *o* |
| 32 | 156 | 232 | 140 | 176 | 225 | | 77 | 62 | 63 | | | 157 | *o* |
| 33 | 79 | 245 | 78 | 134 | | 170 | 35 | 45 | 51 | 29 | 123 | 120 | *s* |
| 34 | 78 | 226 | 86 | 152 | 198 | 197 | 11 | 18 | 57 | 37 | 130 | 115 | *e* |
| 35 | 76 | 254 | 67 | 132 | 187 | 189 | | .. | . | . | 91 | 102 | . |
| 36 | 73 | *287* | 61 | 140 | 171 | 178 | .. | .. | .. | 35 | 70 | 81 | .. |
| 37 | 75 | 178 | 72 | 108 | 141 | 159 | . | .. | . | 36 | | 72 | . |
| 38 | | | . | . | 107 | 137 | . | .. | . | . | . | 101 | .. |
| 39 | 69 | 99 | 77 | 82 | 93 | | .. | .. | | . | 76 | 100 | .. |
| 40 | 66 | 88 | 75 | 76 | .. | 99 | | .. | .. | . | | 125 | .. |
| 41 | | . | . | | 71 | 89 | .. | .. | . | . | . | . | . |
| 42 | 68 | 74 | 37 | 60 | 72 | . | .. | .. | . | . | .. | | . |
| 43 | 62 | 82 | 17 | 54 | 69 | 83 | | . | . | . | | . | .. |
| 44 | 46 | 60 | 5 | 37 | 58 | 88 | . | .. | .. | . | | . | |
| 45 | 37 | 57 | 2 | 32 | . | . | .. | . | | .. | | .. | .. |
| 46 | 32 | 41 | .. | . | | . | . | . | .. | .. | . | .. | .. |
| 47 | 23 | 40 | . | .. | . | .. | . | . | | | .. | . | |
| 48 | 17 | 25 | .. | . | . | .. | . | . | .. | .. | | .. | .. |
| 49 | 5 | 10 | .. | 5 | . | .. | .. | . | . | . | .. | | |
| 50 | .. | .. | 3 | 1 | .. | . | | .. | .. | . | | . | . |

## DESCRIPTION OF CULTURES OF TABLE I

1. Normal population growth in milk bottle of 190 c c. volume.
2. ,, ,, ,, ,, ,, ,,
3. ,, ,, ,, ,, ,, ,,
4. Normal population growth (average of 1–3). ,,
5. Normal population growth with immigration of 6 adult flies from the 3rd to 8th day.
6. ,, ,, ,, ,, ,, of 30 adult flies on the 3rd day.
7. Population growth in cylinder with 26 4 c c. agar–149 6 c c. air-space.
8. ,, ,, ,, 26 4 ,, 74 8 ,,
9. ,, ,, ,, 52·8 ,, 74 8 ,,
10. ,, ,, Erlenmeyer flask with 85 c.c. agar– 40 c.c. air-space.
11. ,, ,, ,, ,, 122 ,, 128 ,,
12. ,, ,, ,, ,, 255 ,, 65 ,,
13. ,, ,, ,, ,, 350 ,, 650 ,,

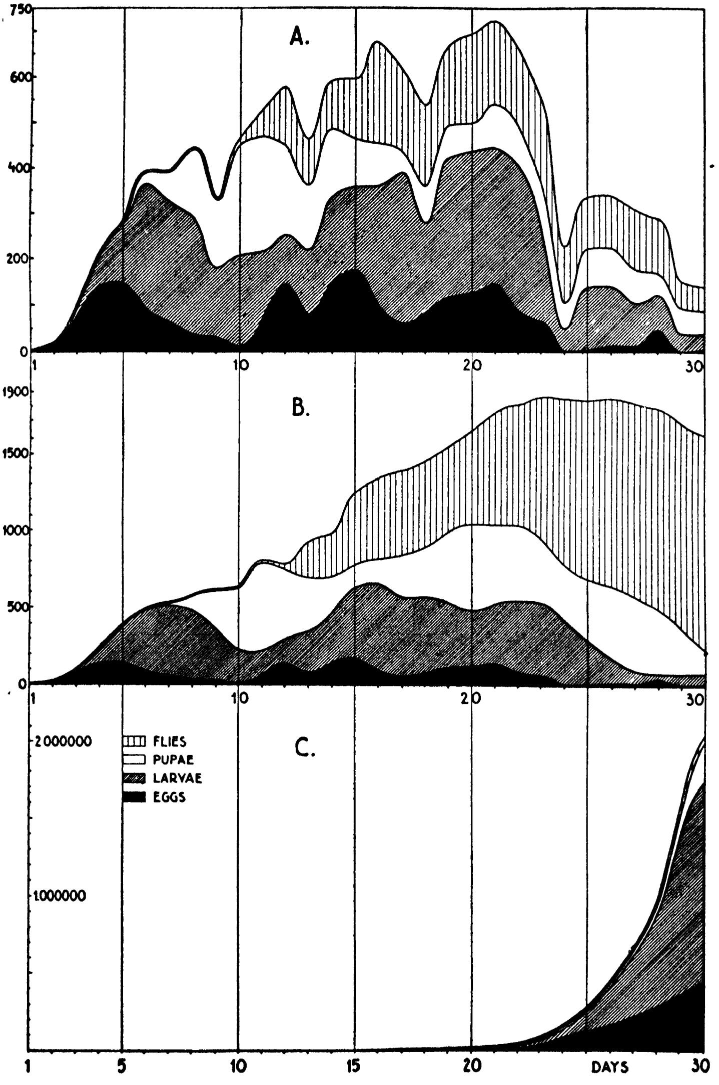


FIG. 12. Population growth in the *Drosophila* bottle. A. As actually observed; B. If all eggs could develop into flies; C. If the population increases under the conditions of the initial growth (13 days adult longevity and 300 eggs per female).

was attempted, therefore, to perform complete daily counts of *Drosophila* of all ages from egg to adult. At first we met with considerable difficulties, since it was difficult to detect eggs and neonate maggots in the banana-agar food-medium. Only after having introduced Pearl's synthetic medium (S – 101), which is clean and transparent, could reliable counts be performed. Owing to this property of the food-medium all complete population counts have been performed on it, though on the whole this food-medium seems to be more unfavourable, at least in the latter half of the culture, to the adults as well as to the development stages.

A culture cannot be continued after it has been counted, as the entire agar is taken out and carefully sliced in order to get a complete census. The experiments were, therefore, arranged by a simultaneous preparation of 90 bottles, each of which was colonized on the same morning by 2 pairs of flies hatched during the 2 hours preceding the transfer. Two bottles were counted and destroyed daily. The course of the experiments demonstrated that quite consistent results were obtained in this way, forming a reliable basis for population analysis. The differences do not surpass those on which Stanley based his complicated and successful mathematical analysis of *Tribolium*-populations, but are rather smaller.[5]

We shall first condense in Table II the results of 4 different series of daily population counts from the beginning to the 32nd day of age. Two series only are counted from the 22nd day on, as the other two breedings were destroyed after that day by mites which fed on the *Drosophila* eggs (Fig. 12, A).

The calculation of the logistic curve proceeds in the usual manner[6] ($d$ = lower asymptote), as given on p. 63.

The results of the parallel calculation for the adult fly population only are shown on p. 63.

The first analysis is based on the daily addition of all stages. Whereas the egg stage lasts almost exactly 1 day, no correction is needed. The daily eggs observed are entered into the column of neonate larvae the following day, of older larvae again the following day, of pupae after 3 further days, of adult flies after 4 additional days, and of mature adult

TABLE II. *Average of four series of breedings of* Drosophila *(from 22nd day two series only)*

| *Day* | *Eggs* | *Neonate larvae* | *Total larvae* | *Pupae* | *Flies living* | *Dead Flies*(c) | | *Total* |
|---|---|---|---|---|---|---|---|---|
| 1 | .. | .. | .. | .. | 4 | .. | | 4 |
| 2 | 16 | .. | .. | .. | 4 | .. | | 20 |
| 3 | 78 | 10 | 10 | .. | 4 | .. | | 92 |
| 4 | 144 | 57 | 65 | .. | 4 | .. | | 213 |
| 5 | 148 | 85 | 134 | .. | 4 | .. | | 268 |
| 6 | 290 | 91 | 257 | 25 | 4 | .. | | 378 |
| 7 | 65 | 62 | 264 | 66 | 4 | .. | | 399 |
| 8 | 38 | 87 | 255 | 150 | 4 | .. | | 447 |
| 9 | 34 | 51 | 152 | 149 | 4 | .. | | 339 |
| 10 | 12 | 58 | 199 | 242 | 15 | .. | | 468 |
| 11 | 76 | 19 | 143 | 250 | 61 | .. | | 530 |
| 12 | 147 | 40 | 109 | 196 | 127 | 5 | 3 | 579 |
| 13 | 83 | 37 | 141 | 139 | 200 | 3 | 4 | 563 |
| 14 | 153 | 61 | 181 | 152 | 204 | 4 | 5 | 690 |
| 15 | 177 | 94 | 183 | 104 | 232 | 16 | 16 | 696 |
| 16 | 99 | 168 | 261 | 94 | *220* | 36 | 20 | 674 |
| 17 | 61 | 150 | 330 | 47 | 181 | 20 | 36 | 619 |
| 18 | 84 | 81 | 196 | 80 | 184 | 85 | 55 | 544 |
| 19 | 118 | 92 | 309 | 71 | 173 | 81 | 81 | 671 |
| 20 | 126 | 92 | 310 | 61 | 193 | 111 | 101 | 690 |
| 21 | 143 | 81 | 297 | 95 | 184 | 172 | 123 | 719 |
| 22 | 88 | 76 | 317 | 88 | *169* | 87 | 149 | 662 |
| 23 | 65 | 38 | 210 | 93 | 183 | 119 | 172 | 551 |
| 24 | .. | 11 | 98 | 53 | 124 | 192 | 185 | 275 |
| 25 | 5 | 12 | 135 | 83 | 112 | 187 | 197 | 235 |
| 26 | 13 | 16 | 128 | 84 | 113 | 166 | 201 | 338 |
| 27 | 13 | 5 | 91 | 75 | *129* | 205 | 250 | 308 |
| 28 | 48 | 3 | 74 | 49 | 118 | 214 | 325 | 289 |
| 29 | .. | .. | 39 | 54 | 59 | 428 | 428 | 152 |
| 30 | 4 | .. | 36 | 48 | 53 | 567 | 507 | 141 |
| 31 | .. | .. | .. | .. | (42) | .. | 532 | 125 |
| 32 | .. | .. | 18 | 60 | 30 | 588 | 588 | 108 |

(c) See note c, p. 180.

flies after 1 day again. The last two columns of Table III (see p. 64) show the number of living adult flies to be expected if the average longevity lasted 13 days, and finally the number of adult flies of reproductive age (2nd to 13th day).

This auxiliary manipulation enables us to make two additional calculations. We shall first calculate the development

| $x$ (*days*) | $y$ (*total population*) | $y-d$ | $k-(y-d)$ | $\frac{k-(y-d)}{y-d}$ | $\log\frac{(k-(y-d)}{y-d}$ |
|---|---|---|---|---|---|
| 1 | 4 | 0 | 719 | ∞ | ∞ |
| 2 | 20 | 16 | 703 | 43·84 | 1·6418 |
| 3 | 92 | 88 | 631 | 7·17 | 0·8555 |
| 4 | 213 | 209 | 510 | 2·44 | 0·3873 |
| 5 | 286 | 274 | 445 | 1·62 | 0·2095 |
| 6 | 378 | 374 | 345 | 0·92 | —0·0362 |
| 7 | 399 | 395 | 324 | 0·82 | —0·0862 |
| 8 | 447 | 443 | 276 | 0·62 | —0·2076 |
| 9 | 339 | 335 | 384 | 1·15 | —0·0607 |
| 10 | 468 | 464 | 255 | 0·55 | —0·2596 |
| 11 | 530 | 526 | 193 | 0·37 | —0·4318 |
| 12 | 579 | 575 | 144 | 0·25 | —0·6021 |
| 13 | 563 | 559 | 160 | 0·29 | —0·5376 |
| 14 | 690 | 686 | 33 | 0·042 | —1·3768 |
| 15 | 696 | 692 | 27 | 0·039 | —1·4089 |
| 16 | 674 | 670 | 49 | 0·073 | —1·1367 |
| 17 | 619 | 615 | 104 | 0·169 | —0·7721 |
| 18 | 544 | 540 | 179 | 0·37 | —0·4318 |
| 19 | 671 | 667 | 52 | 0·078 | —1·1079 |
| 20 | 690 | 686 | 33 | 0·048 | —1·3188 |
| 21 | 719 | 715 | 4 | 0·006 | —2·2218 |

$$
\begin{aligned}
a+\ \ 4b &= \quad 0{\cdot}5\times 2{\cdot}3026 = \quad 1{\cdot}1513\\
a+12b &= -0{\cdot}7\times 2{\cdot}3026 = -1{\cdot}6182\\
\hline
8b &= -2{\cdot}87312\\
b &= -0{\cdot}3591\\
a &= 2{\cdot}3877
\end{aligned}
$$

$$y = \frac{719}{1+e^{2\cdot3877-0\cdot3591x}}.$$

| $x$ | $y$ | $y-d$ | $k-(y-d)$ | $\frac{k-(y-d)}{y-d}$ | $\log\frac{(k-(y-d)}{y-d}$ |
|---|---|---|---|---|---|
| 1 | 4 | 0 | 232 | ∞ | ∞ |
| 9 | 4 | 0 | 232 | ∞ | ∞ |
| 10 | 15 | 11 | 221 | 20·09 | 1·303 |
| 11 | 61 | 57 | 175 | 3·07 | 0·4871 |
| 12 | 127 | 123 | 109 | 0·88 | —0·0555 |
| 13 | 200 | 196 | 36 | 0·18 | —0·7447 |
| 14 | 204 | 200 | 32 | 0·16 | —0·7958 |
| 15 | 232 | 228 | 4 | 0·018 | —1·7447 |

$a = 17{\cdot}0159 \qquad b = -\ 1{\cdot}4019$

$$y = \frac{232}{1+e^{17\cdot0159+1\cdot4019x}}.$$

## TABLE III. *Daily addition of all stages of* Drosophila *(I–IV)*

| *Day* | *Eggs* | *Neonate larvae* | *Larvae II to III* | *Pupae* | *Flies* | *Living (13 days)* | *Living*(d) *(2–13 days)* |
|---|---|---|---|---|---|---|---|
| 1 | .. | .. | .. | .. | 4 | 4 | .. |
| 2 | 16 | .. | .. | .. | .. | 4 | 4 |
| 3 | 78 | 16 | .. | .. | .. | 4 | 4 |
| 4 | 144 | 78 | 16 | .. | .. | 4 | 4 |
| 5 | 148 | 144 | 78 | .. | .. | 4 | 4 |
| 6 | 92 | 148 | 144 | .. | .. | 4 | 4 |
| 7 | 65 | 92 | 148 | 16 | .. | 4 | 4 |
| 8 | 38 | 65 | 92 | 78 | .. | 4 | 4 |
| 9 | 34 | 38 | 65 | 144 | .. | 4 | 4 |
| 10 | 12 | 34 | 38 | 148 | .. | 4 | 4 |
| 11 | 76 | 12 | 34 | 92 | 16 | 20 | 4 |
| 12 | 147 | 76 | 12 | 65 | 78 | 98 | 20 |
| 13 | 83 | 147 | 76 | 38 | 144 | 242 | 98 |
| 14 | 153 | 83 | 147 | 34 | 148 | 388 | 242 |
| 15 | 177 | 153 | 83 | 12 | 92 | 480 | 388 |
| 16 | 99 | 177 | 153 | 76 | 65 | 545 | 480 |
| 17 | 61 | 99 | 177 | 147 | 38 | 583 | 545 |
| 18 | 84 | 61 | 99 | 83 | 34 | 617 | 583 |
| 19 | 118 | 84 | 61 | 153 | 12 | 629 | 617 |
| 20 | 126 | 118 | 84 | 177 | 76 | 705 | 629 |
| 21 | 143 | 126 | 118 | 99 | 147 | 852 | 705 |
| 22 | 88 | 143 | 126 | 61 | 83 | 935 | 852 |
| 23 | 65 | 88 | 143 | 84 | 153 | 1,088 | 935 |
| 24 | .. | 65 | 88 | 118 | 177 | 1,249 | 1,088 |
| 25 | 5 | .. | 65 | 126 | 99 | 1,270 | 1,249 |
| 26 | 13 | 5 | .. | 143 | 61 | 1,187 | 1,270 |
| 27 | 13 | 13 | 5 | 88 | 84 | 1,123 | 1,187 |
| 28 | 48 | 13 | 13 | 65 | 118 | 1,149 | 1,123 |
| 29 | .. | 48 | 13 | .. | 126 | 1,210 | 1,149 |
| 30 | 4 | .. | 48 | 5 | 143 | 1,260 | 1,210 |
| 31 | .. | 4 | .. | 13 | 88 | 1,291 | 1,260 |
| 32 | .. | .. | 4 | 13 | 65 | 1,279 | 1,291 |

(d) See note d, p. 180.

of the *Drosophila* population, if all eggs developed into flies (Table IV, Fig. 12, B), and furthermore the potential development of *Drosophila* in the milk bottle, if the initial conditions of the first pair continued to exist throughout the breeding with 13 days adult longevity and 25 eggs daily per female on the 2nd to 13th day of life (Table V, Fig. 12, c).

TABLE IV. *Development of* Drosophila *population (I–IV), if all eggs would develop into flies*

| Day | Eggs (1 day) | Larvae I (1 day) | Larvae II–III (3 days) | Pupae | Adults |  |  | Total |
|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Total | Dead | Living |  |
| 1 | .. | .. | .. | .. | 4 | .. | 4 | 4 |
| 2 | 16 | .. | .. | .. | 4 | .. | 4 | 20 |
| 3 | 78 | 16 | .. | .. | 4 | .. | 4 | 98 |
| 4 | 144 | 78 | 16 | .. | 4 | .. | 4 | 242 |
| 5 | 148 | 144 | 94 | .. | 4 | .. | 4 | 390 |
| 6 | 92 | 148 | 238 | .. | 4 | .. | 4 | 482 |
| 7 | 65 | 92 | 360 | 16 | 4 | .. | 4 | 537 |
| 8 | 38 | 65 | 384 | 94 | 4 | .. | 4 | 581 |
| 9 | 34 | 38 | 305 | 238 | 4 | .. | 4 | 619 |
| 10 | 12 | 34 | 195 | 386 | 4 | .. | 4 | 631 |
| 11 | 76 | 12 | 137 | 452 | 16 | .. | 16 | 693 |
| 12 | 147 | 76 | 84 | 449 | 94 | 3 | 91 | 847 |
| 13 | 83 | 147 | 122 | 343 | 238 | 4 | 234 | 929 |
| 14 | 153 | 83 | 235 | 229 | 386 | 5 | 281 | 971 |
| 15 | 177 | 153 | 306 | 149 | 478 | 16 | 462 | 1,247 |
| 16 | 99 | 177 | 383 | 160 | 543 | 20 | 523 | 1,342 |
| 17 | 61 | 99 | 413 | 269 | 581 | 36 | 545 | 1,387 |
| 18 | 84 | 61 | 429 | 318 | 615 | 55 | 560 | 1,452 |
| 19 | 118 | 84 | 337 | 459 | 627 | 81 | 546 | 1,544 |
| 20 | 126 | 118 | 244 | 560 | 703 | 101 | 602 | 1,650 |
| 21 | 143 | 126 | 263 | 512 | 850 | 123 | 727 | 1,831 |
| 22 | 88 | 143 | 320 | 490 | 933 | 149 | 784 | 1,825 |
| 23 | 65 | 88 | 387 | 421 | 1,086 | 172 | 914 | *1,875* |
| 24 | .. | 65 | 357 | 362 | 1,263 | 185 | 1,087 | 1,862 |
| 25 | 5 | .. | 296 | 389 | 1,362 | 197 | 1,165 | 1,855 |
| 26 | 13 | 5 | 153 | 463 | 1,423 | 201 | 1,222 | 1,856 |
| 27 | 13 | 13 | 70 | 475 | 1,507 | 250 | 1,257 | 1,828 |
| 28 | 48 | 13 | 18 | 422 | 1,625 | 325 | 1,300 | 1,801 |
| 29 | .. | 48 | 31 | 296 | 1,751 | 428 | 1,323 | 1,698 |
| 30 | 4 | .. | 74 | 158 | 1,894 | 507 | 1,387 | 1,623 |
| 31 | .. | 4 | 61 | 83 | 1,982 | 532 | 1,450 | 1,598 |
| 32 | .. | .. | 52 | 31 | 2,047 | 588 | 1,459 | 1,542 |

In analysing the three basic tables, that of the potential development, when initial conditions continue to prevail, needs little comment. It exposes the typical exponential curve of unlimited growth.

The table in which *all* eggs are assumed to develop into flies is of interest because it shows that even with a steadily

TABLE V. *Potential development if the conditions available for the first two pairs continued to exist throughout the breeding*

| *Day* | *Eggs* (*1 day*) | *Larvae* (*4 days*) | *Pupae* (*4 days*) | *Flies* (*13 days*) | | | *Total* |
|---|---|---|---|---|---|---|---|
| | | | | *Total* | *Dead* | *Living* | |
| 1 | .. | .. | .. | .. | .. | 4 | 4 |
| 2 | 50 | .. | .. | 4 | .. | 4 | 54 |
| 3 | 50 | 50 | .. | 4 | .. | 4 | 104 |
| 4 | 50 | 100 | .. | 4 | .. | 4 | 154 |
| 5 | 50 | 150 | .. | 4 | .. | 4 | 204 |
| 6 | 50 | 200 | .. | 4 | .. | 4 | 254 |
| 7 | 50 | 200 | 50 | 4 | .. | 4 | 304 |
| 8 | 50 | 200 | 100 | 4 | .. | 4 | 354 |
| 9 | 50 | 200 | 150 | 4 | .. | 4 | 404 |
| 10 | 50 | 200 | 200 | 4 | .. | 4 | 454 |
| 11 | 50 | 200 | 200 | 54 | .. | 54 | 504 |
| 12 | 675 | 200 | 200 | 104 | .. | 104 | 1,179 |
| 13 | 1,300 | 825 | 200 | 154 | .. | 154 | 2,479 |
| 14 | 1,800 | 2,075 | 200 | 204 | 4 | 200 | 4,275 |
| 15 | 2,500 | 3,825 | 200 | 254 | 4 | 250 | 6,775 |
| 16 | 3,125 | 6,275 | 200 | 304 | 4 | 300 | 9,900 |
| 17 | 3,750 | 8,725 | 825 | 354 | 4 | 350 | 13,650 |
| 18 | *4,375* | 11,175 | 2,075 | 404 | 4 | *400* | 18,025 |
| 19 | 5,000 | 13,750 | 3,826 | 454 | 4 | 450 | 23,025 |
| 20 | 5,625 | 16,250 | 6,275 | 504 | 4 | 500 | 28,650 |
| 21 | 6,250 | 18,750 | 8,725 | 1,179 | 4 | *1,175* | 34,900 |
| 22 | 14,100 | 21,250 | 11,175 | 2,479 | 4 | 2,475 | 49,000 |
| 23 | 30,950 | 30,975 | 13,750 | 4,279 | 4 | 4,275 | 79,950 |
| 24 | 83,875 | 56,925 | 16,250 | 6,779 | 54 | 6,725 | 163,775 |
| 25 | 122,500 | 125,175 | 18,750 | 9,904 | 104 | 9,800 | 276,225 |
| 26 | 168,750 | 251,425 | 21,250 | 13,654 | 154 | *13,500* | 454,925 |
| 27 | 223,825 | 396,075 | 30,975 | 18,029 | 204 | 17,825 | 668,700 |
| 28 | 284,700 | 598,950 | 56,925 | 23,029 | 254 | 22,775 | 963,350 |
| 29 | 354,375 | 1,031,650 | 125,175 | 28,654 | 304 | 28,350 | 1,539,550 |
| 30 | 431,875 | 1,294,775 | 251,425 | 34,904 | 354 | 34,550 | 2,012,625 |

increasing number of adult flies oviposition would cease by force of density-pressure alone.

The table representing the actual census needs some further explanation. The maxima of the different stages occur as follows (table on p. 67):

Three different egg maxima occur on the 5th, 15th, and 21st days, more or less coinciding with or closely preceding the peaks of the fly population. The first maximum indicates the peak of the parent oviposition. The larval maxima follow those of the eggs 1 day later, and those of the pupa 4 days later. It seems that pupal and perhaps also later larval development is often retarded under unfavourable conditions (such as overcrowding). This would explain the irregularities occurring in adult hatching.

| *Age in days:* | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* | *14* | *15* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Eggs . . | .. | .. | .. | .. | 148 | .. | .. | .. | .. | .. | .. | .. | .. | .. | 177 |
| Larvae . | .. | .. | .. | .. | .. | .. | 264 | .. | .. | .. | .. | .. | .. | .. | .. |
| Pupae . | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 250 | .. | .. | .. | .. |
| Adults . | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 232 |
| Deaths . | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Total population . | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | 696 |

| *Age in days:* | *16* | *17* | *18* | *19* | *20* | *21* | *22* | *23* | *24* | *25* | *26* | *27* | *28* | *29* | *30* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Eggs . . | .. | .. | .. | .. | .. | 143 | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Larvae . | .. | 330 | .. | .. | .. | .. | 317 | .. | .. | .. | .. | .. | .. | .. | .. |
| Pupae . | .. | .. | .. | .. | .. | 95 | .. | .. | .. | .. | 84 | .. | .. | .. | .. |
| Adults . | .. | .. | .. | .. | 193 | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Deaths . | .. | .. | .. | 26 | .. | .. | 26 | .. | .. | .. | .. | .. | .. | 103 | .. |
| Total population . | .. | .. | .. | .. | .. | 719 | .. | .. | .. | .. | .. | .. | .. | .. | .. |

The mortality is, on the average, as follows: commencing with 1,000 eggs we obtain:

|  | *Eggs* | *Neonate larvae* | *Older larvae* | *Pupae* | *Adults* |
|---|---|---|---|---|---|
| Living | 1,000 | 752 | 519 | 306 | 305 individuals |
| Mortality in % | 24·8 | 31·0 | 41·0 | 0·3 | (Total 69·5 %) |

Mortality is very irregularly distributed, when adult hatching is correlated with the corresponding value of eggs, as may be gathered from the following list:

| Day . . | 2/3 | 4/5 | 6/7 | 8/9 | 10/11 | 12/13 | 14/15 | 16/17 | 18/19 | 20/21 | 22/23 | 24/25 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ratio $\frac{\text{adults hatched}}{\text{eggs}}$ | 0·59 | 0·49 | 0·30 | 0·17 | 0·18 | 0·13 | 0·03 | 0·02 | 0·35 | 0·41 | 0·57 | (8.80) |

This phenomenon is probably best explained by retarded hatching and development, for which reason the initially correct analysis correlations grow more and more unsuitable for calculation, when the overlapping and accumulation of these retardations makes itself felt.

The data concerning the change of adult physiology with progression of age of the *Drosophila* culture are compiled in the following table and are also shown in Fig. 13.

TABLE VI. *Change of adult physiology with progression of age of* Drosophila *culture*

| *Age of culture in days* | *No. of living adult flies* | *Daily addition of adult flies (smoothed)* | *Daily deaths of adult flies (smoothed)* | *No. of breeding females per bottle* | *Longevity in days* | *Total no. of daily eggs* | *No. of eggs per female-day* |
|---|---|---|---|---|---|---|---|
| 1 | 4 | .. | .. | 2 | 13·0 | .. | .. |
| 2 | 4 | .. | .. | 2 | .. | 16 | 8·0 |
| 3 | 4 | .. | .. | 2 | .. | 78 | 39·0 |
| 4 | 4 | .. | .. | 2 | .. | 144 | 72·0 |
| 5 | 4 | .. | .. | 2 | .. | 148 | 74·0 |
| 6 | 4 | .. | .. | 2 | .. | 92 | 46·0 |
| 7 | 4 | .. | .. | 2 | .. | 65 | 32·5 |
| 8 | 4 | .. | .. | 2 | .. | 38 | 19·0 |
| 9 | 4 | .. | .. | 2 | .. | 34 | 17·0 |
| 10 | 15 | 11 | .. | 2 | 4·0 | 12 | 6·0 |
| 11 | 61 | 46 | .. | 9 | 5·1 | 76 | 8·4 |
| 12 | 127 | 69 | 3 | 37 | 9·4 | 147 | 4·0 |
| 13 | 200 | 74 | 1 | 76 | 11·0 | 83 | 1·09 |
| 14 | 204 | 5 | 1 | 120 | 10·0 | 153 | 1·28 |
| 15 | 232 | 9 | 11 | 123 | 9·9 | 177 | 1·44 |
| 16 | 220 | 2 | 4 | 139 | 9·0 | 99 | 0·71 |
| 17 | 181 | 1 | 16 | 132 | 8·0 | 61 | 0·46 |
| 18 | 184 | 18 | 19 | 109 | 8·8 | 84 | 0·77 |
| 19 | 173 | 15 | 26 | 110 | 9·7 | 118 | 1·07 |
| 20 | 193 | 30 | 20 | 104 | 9·0 | 126 | 1·16 |
| 21 | 184 | 9 | 22 | 116 | 8·0 | 143 | 1·20 |
| 22 | 169 | 8 | 26 | 110 | 7·0 | 88 | 0·80 |
| 23 | 183 | 6 | 23 | 101 | 6·0 | 65 | 0·64 |
| 24 | 124 | 2 | 13 | 110 | 5·0 | 0 | 0·00 |
| 25 | 112 | 0 | 12 | 74 | 4·0 | 5 | 0·07 |
| 26 | 113 | 5 | 4 | 67 | 3·0 | 13 | 0·19 |
| 27 | 129 | 65 | 49 | 68 | 2·0 | 13 | 0·19 |
| 28 | 118 | 66 | 75 | 87 | 1·0 | 48 | 0·55 |
| 29 | 58 | 44 | 103 | 71 | 0·43 | 0 | 0·00 |
| 30 | 53 | 73 | 79 | 35 | 0·39 | 4 | 0·11 |
| 31 | 42 | 14 | 25 | 32 | .. | 0 | 0·00 |
| 32 | 30 | 44 | 56 | 25 | .. | 0 | 0·00 |

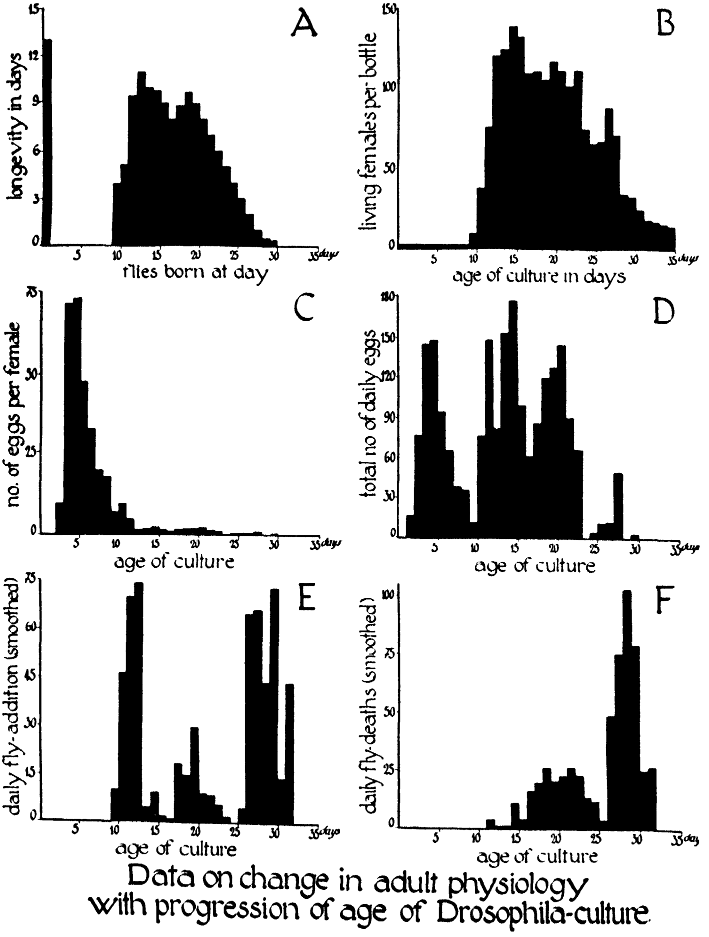


FIG. 13. Change of adult physiology with progression of age in *Drosophila* culture. A. Adult longevity; B. Total eggs laid daily; C. Eggs per female-day; D. Number of breeding females per bottle; E. Daily addition of adult flies; F. Daily deaths of adult flies.

The actual oviposition per female-day is given on p. 70.

The 2 females of the parent generation deposited about 300 eggs per female, which gives 23·1 eggs per female-day (including the first day or the pre-oviposition period). The

| *Age of culture in days* | *Average eggs per female-day* | *Average females per bottle* |
|---|---|---|
| 1–5 | 38·6 | 2·0 |
| 6–10 | 24·1 | 2·0 |
| 11–15 | 3·24 | 73·0 |
| 16–20 | 0·83 | 118·8 |
| 21–5 | 0·55 | 102·2 |
| 26–30 | 0·21 | 65·6 |
| 31–5 | 0·00 | 18·2 |

other 370 females deposited 1,530 eggs, i.e. 4·13 eggs per female or 0·71 eggs per female-day.

Comparing the results of Tables II, IV, and V, the fertility is as follows:

| | *Eggs per female* | *Eggs per female-day* |
|---|---|---|
| Actually observed . . . | 5·72 | 0·975 |
| If all eggs develop to maturity . | 1·73 | 0·198 |
| If the initial conditions continue | 83·53 | 20·268 |

For the calculation of adult longevity we use the data of the first series only. The average longevity of the flies born on each date is compiled in Table VI.

Neglecting the short longevity of the first-born adults of the filial generations, probably due to the fact that our calculation has assumed that the flies die in the sequence of their birth (not yet having been individually marked), it is obvious that with the progress of age the adult longevity decreases steadily. The final break-down, leading to death before even sexual maturity has been attained, is due to intoxication and not to density alone.

The change of the age structure in the *Drosophila* bottle is illustrated by the figures on p. 71 and in Fig. 4, B.

The growing population is almost pyramid-shaped, the stable population bell-shaped, and the contracting population urn-shaped in age structure. This is the structure known from human populations as well as from bee populations. In our present analysis the age-structure is of special interest, because it confirms our opinion that the logistic curve of population growth within the *Drosophila* bottle is really a superposition of two growth-periods. On the 10th day the age-structure shows the first beginning of a dwindling population, whereas on the 15th and 20th days the pyramid shape is again restored, after the oviposition of the adults of the first filial generation has started. On the 25th day dwindling has started again, and now leads to the final contraction, the progression of which is well illustrated by the age-structure on the 30th and still more so on the 35th day.

| *Age of culture in days* | *No. of eggs* | *No. of neonate maggots* | *No. of older maggots* | *No. of pupae* | *No. of adults* | *Total population* |
|---|---|---|---|---|---|---|
| 5 | 148 | 85 | 49 | .. | 4 | 286 |
| 10 | 12 | 58 | 141 | 242 | 15 | 468 |
| 15 | 177 | 94 | 89 | 104 | 232 | 696 |
| 20 | 126 | 92 | 218 | 61 | 193 | 690 |
| 25 | 5 | 12 | 123 | 83 | 112 | 335 |
| 30 | 4 | .. | 36 | 48 | 53 | 141 |
| 35 | .. | .. | 21 | 52 | 25 | 98 |

Or in percentages:

| *Age of culture in days* | *No. of eggs* | *No. of neonate maggots* | *No. of older maggots* | *No. of pupae* | *No. of adults* | *Total population* |
|---|---|---|---|---|---|---|
| 5 | 52 | 30 | 17 | .. | 2 | 101 |
| 10 | 3 | 13 | 30 | 52 | 3 | 101 |
| 15 | 25 | 14 | 13 | 15 | 34 | 101 |
| 20 | 18 | 13 | 31 | 9 | 28 | 99 |
| 25 | 1 | 4 | 37 | 25 | 33 | 100 |
| 30 | 3 | .. | 25 | 34 | 38 | 100 |
| 35 | .. | .. | 21 | 52 | 27 | 100 |

## 5. DYNAMICS OF POPULATION GROWTH AND DECREASE IN THE *Drosophila* BOTTLE

Gause[8] has made a first attempt to analyse the dynamics of population increase of *Paramaecium caudatum*. The calculation is very simple in this case, because every individual is reproducing at regular intervals, whereas the reproduction of *Drosophila* is concentrated in a certain age. Only the individuals of that age oviposit, and there exists no fixed correlation between the number of individuals in the reproductive age and the total population abundance. We must, therefore, make considerable changes in the formulae necessary for calculation, still more so as we desire to analyse the actual population change for all 30 days, not for the increase only.

Table VII compiles all necessary data and calculations. Columns A and B give the total population number and that of adult flies in the reproductive age. Column C shows the potential increase of the population per day. Whereas 60 per cent. of the flies are females and 25 eggs are laid per female-day from the 2nd to the 13th day of life, this value is obtained by multiplying the value in column B by 15(e). Column D contains the actual number of eggs laid daily. Column E, the degree of realization of the potential increase, is the ratio

$$\frac{\text{actually laid eggs per day (D)}}{\text{potential no. of eggs (C)}}.$$

The environmental resistance (column F) is then 1 — environmental resistance. The rate of growth (column G) is calculated as the quotient of growth, i.e. the ratio

$$\frac{\text{total population}}{\text{total population of previous day}}.$$

This seems to give a better value for ratio of growth than that obtained by Gause. Gause has represented the accumulative distribution curve as that of rate of growth, which seems to be unjustified. The intensity of struggle for existence (column H) is obtained as

$$\frac{\text{potential increase of population rate of growth}}{\text{rate of growth}}.$$

All of the basic formulae used in these calculations are simpler and, it seems, equally useful for representing symbolically the dynamics of the population trend. The conception of realization of potential increase is fundamentally different from that of Gause; the two curves are therefore not directly comparable.

The potential increase of the *Drosophila* population is proportional to the number of flies in the reproductive age.

(e) See note e, p. 180.

TABLE VII. *Dynamic changes in the* Drosophila *bottle.*

| *Day* | *A* *Total population* (*y*) | *B* *Flies in reproductive age* | C(e) *Potential increase of population* | *D* *Daily actual no. of eggs* | *E* *Realization of potential increase* | *F* *Environmental resistance* | G *Rate of growth* | *H* *Intensity of struggle for existence* |
|---|---|---|---|---|---|---|---|---|
| 1 | 4 | . . | . . | . . | 0·00 | 0·00 | 0 | 0 |
| 2 | 20 | 4 | 50 | 16 | 0·32 | —0·68 | 5·0 | 9·0 |
| 3 | 92 | 4 | 50 | 78 | 1·56 | —0·56 | 4·6 | 9·7 |
| 4 | 213 | 4 | 50 | 144 | 2·88 | —1·88 | 2·3 | 2·1 |
| 5 | 286 | 4 | 50 | 148 | 2·96 | —1·96 | 1·3 | 3·7 |
| 6 | 378 | 4 | 50 | 92 | 1·84 | —0·84 | 1·3 | 3·7 |
| 7 | 399 | 4 | 50 | 65 | 1·30 | —0·30 | 1·1 | 4·4 |
| 8 | 447 | 4 | 50 | 38 | 0·76 | —0·24 | 1·1 | 4·4 |
| 9 | 339 | 4 | 50 | 34 | 0·68 | 0·32 | 0·7 | 7·0 |
| 10 | 468 | 4 | 50 | 12 | 0·24 | 0·76 | 1·4 | 3·5 |
| 11 | 530 | 15 | 225 | 76 | 0·30 | 0·70 | 1·1 | 207 |
| 12 | 579 | 61 | 915 | 147 | 0·16 | 0·84 | 1·1 | 822 |
| 13 | 563 | 127 | 1,905 | 83 | 0·041 | 0·959 | 1·0 | 1,904 |
| 14 | 690 | 200 | 3,000 | 153 | 0·051 | 0·949 | 1·2 | 2,499 |
| 15 | 696 | 204 | 3,060 | 177 | 0·058 | 0·942 | 1·0 | 3,059 |
| 16 | 674 | 232 | 3,480 | 99 | 0·028 | 0·972 | 1·0 | 3,479 |
| 17 | 619 | 220 | 3,300 | 61 | 0·018 | 0·982 | 0·9 | 3,666 |
| 18 | 544 | 181 | 2,715 | 84 | 0·031 | 0·969 | 0·9 | 3,016 |
| 19 | 671 | 184 | 2,760 | 118 | 0·043 | 0·957 | 1·2 | 2,299 |
| 20 | 690 | 173 | 2,595 | 126 | 0·049 | 0·951 | 1·0 | 2,594 |
| 21 | 719 | 193 | 2,795 | 143 | 0·051 | 0·949 | 1·0 | 2,794 |
| 22 | 662 | 184 | 2,760 | 88 | 0·032 | 0·968 | 0·9 | 3,066 |
| 23 | 551 | 169 | 2,535 | 65 | 0·022 | 0·978 | 0·9 | 2,817 |
| 24 | 275 | 183 | 2,745 | 0 | 0 | 1·000 | 0·5 | 5,489 |

## ERRATUM

P. 72. ll. 17–18, *for* ‘environmental resistance’
*read* ‘degree of realization of potential increase’.

tion. The values over 1·0 observed from the 3rd to 7th day

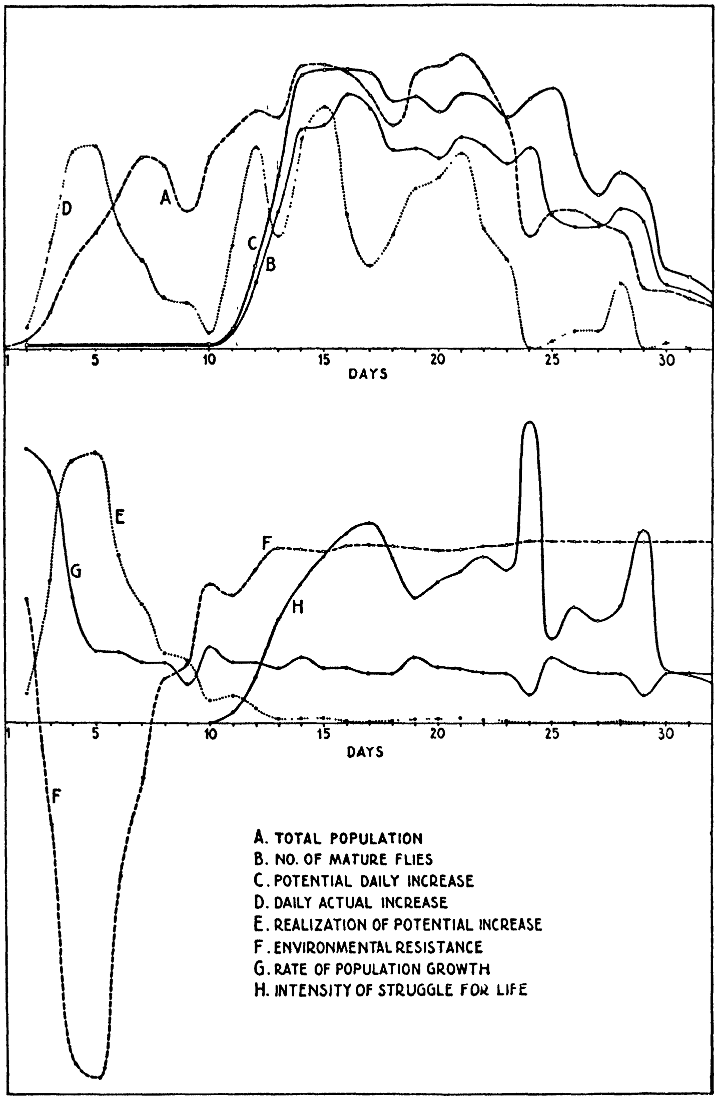


FIG. 14. Dynamics of population growth and decrease in the *Drosophila* bottle. A. Total population; B. Number of adult flies in the reproductive age; C. Daily potential increase of population; D. Daily actual number of eggs laid; E. Degree of realization of the potential increase; F. Environmental resistance; G. Rate of population growth; H. Intensity of struggle for existence.

are caused by massed oviposition in those days, the total egg-production (=300 eggs per female) remaining constant. Correspondingly, the environmental resistance shows negative values during the same period. It grows steadily from 0 to values approaching 1·0 rather closely. The rate of growth is highest at its beginning, and from the 22nd day on falls below the maintenance (=below 1·0). The daily deficit is small, but accumulates quite quickly. The intensity of the struggle for existence is very low as long as only the adults of the paternal generation exist. With the beginning of oviposition in the filial generation, the struggle for existence grows rapidly and follows in its intensity an exponential curve until the first maximum is reached on the 15th to 17th day. Later it passes to its absolute maximum, when the heavy drop in total population begins; as a rule, it grows smaller steadily afterwards. This indicates clearly that it is not the struggle for existence which enforces the dying out of the *Drosophila* culture, but an extrinsic factor, which seems to be an intoxication of some sort, still unknown in its specific nature.

We may now divide the life-history of the *Drosophila* culture in our milk bottles into the following four periods:

I. *Period of initial growth.* 0–10 days. Adult population low, immature stages increasing rapidly. Rate of growth steadily declining. Environmental resistance and intensity of struggle for existence very low. The potential increase is more or less realized.

II. *Period of rapid growth.* From 10th to 14th day. The adult population rapidly approaches its maximum, the total population its first peak. The increase of immature stages slackens down considerably, whereas the rate of growth is always slightly above the maintenance value only. Environmental resistance and intensity of struggle for existence have rapidly grown and approach maximal values. The potential increase is not progressive any longer.

III. *Period of oscillations around the stable maximum.* From 15th to 22nd day. The total as well as the adult population fluctuate between values of (80–) 90–100 per cent. of the upper asymptote. The increase of immature stages and realization of potential increase remain approximately as in the previous period. The rate of growth fluctuates about the maintenance value. Environmental resistance and struggle for existence have attained their maximum and remain fairly stable.

IV. *Period of contraction.* From 23rd to 35th (–40th) day. Total as well as adult population decrease steadily, also the number of immature stages and the realization of the potential increase. Both later columns approach zero at the end of the period, the adults being the last to die out. Rate of growth is in consequence always below the maintenance value. Environmental resistance is about 100 per cent., whereas intensity of struggle for existence falls below the maximum value. The final contraction is therefore not due to the intra-specific struggle for existence, but to an extrinsic factor. This factor does not seem to be lack of food, but some intoxication, especially effective in the adult stage. The enormous mortality following hatching of new flies during the latter part of this period before the end of their first day of adult life points to this direction. Population pressure is certainly not involved in this adult mortality, or only to an inconsiderable extent. More detailed studies are needed before any explanation may be given. The form of decrease agrees with that of a moderate intoxication curve.

## 6. COMPARISON AND CONCLUSIONS

This analysis of growth of *Drosophila* populations may be compared with the population of two other insects growing in a limited space.

We shall begin with Chapman's classical experiments on the flour beetle *Tribolium confusum* and the able analysis and variation of these experiments by Stanley, Holdaway, Park, and others.[9] Table VIII gives the comparative analysis for this beetle bred at 32° C. and 75 per cent. R.H. The constants are as follows: egg 4·42 days; larva 17·34 days; pupa 5·38 days; eggs per female-day 10·73; sex-ratio about equal.

The analysis shows that within the period of observation 298,679 eggs should have been laid. 22,631 eggs, i.e. 7·6 per cent. of the potential egg-production were counted. From these 22,631 eggs 1,079 larvae hatched, of which

601 pupated. Between 386 to 600 adults hatched from these eggs, probably about 400.

Following the observation that larvae and adults of *Tribolium* willingly eat their own eggs (but do not search after such food!), Chapman and his co-workers concluded that the increased chance of meeting eggs leads to a constant heavy decimation which is the real reason for the stable adult population often observed for quite a considerable period in these experiments. We may assume that the difference between eggs actually laid and the number of larvae observed is due largely to feeding of the adults on the eggs. But even if, in addition, the same amount or twice as much is destroyed in this way, only a fraction of the potential

TABLE VIII. *Population trend and analysis of* Tribolium confusum *at* 32° *C.*

| Day | *A*<br>*Total population* | *B*<br>*Adult population* | *C*<br>*Potential increase of population* | *D*<br>*Actual no. of eggs per day* | *E*<br>*Realization of potential increase* | *F*<br>*Environmental resistance* | G<br>*Rate of growth* | *H*<br>*Intensity of struggle for existence* |
|---|---|---|---|---|---|---|---|---|
| 0 | 16 | 16 | .. | .. | .. | 0·0 | ∞ | .. |
| 10 | 568 | 15 | 858 | 802 | 934 | 0·066 | 35·5 | 23·2 |
| 20 | 563 | 14 | 751 | 237 | 315 | 0·685 | 1·0 | 750 |
| 30 | 596 | 92 | 2,468 | 168 | 0·068 | 0·932 | 1·1 | 2,243 |
| 40 | 760 | 350 | 9,389 | 127 | 0·013 | 0·987 | 1·3 | 7,221 |
| 50 | 791 | 362 | 7,769 | 344 | 0·044 | 0·056 | 1·1 | 7,062 |
| 60 | 844 | 373 | 20,065 | 1,040 | 0·050 | 0·950 | 1·1 | 17,331 |
| 70 | 1,056 | 362 | 19,421 | 1,559 | 0·080 | 0·920 | 1·3 | 14,938 |
| 80 | 1,138 | 364 | 19,529 | 1,722 | 0·088 | 0·912 | 1·1 | 17,753 |
| 90 | 1,286 | 361 | 19,421 | 2,068 | 0·106 | 0·894 | 1·1 | 17,655 |
| 100 | 1,299 | 357 | 19,207 | 2,106 | 0·109 | 0·891 | 1·0 | 19,206 |
| 110 | 1,498 | 350 | 18,777 | 2,515 | 0·134 | 0·866 | 1·2 | 15,648 |
| 120 | 1,095 | 350 | 18,777 | 1,471 | 0·078 | 0·922 | 0·7 | 26,823 |
| 130 | 1,013 | 343 | 18,455 | 1,340 | 0·072 | 0·928 | 0·9 | 20,505 |
| 140 | 1,213 | 325 | 17,489 | 1,887 | 0·108 | 0·892 | 1·2 | 14,573 |
| 150 | 1,137 | 319 | 17,168 | 1,652 | 0·096 | 0·904 | 0·9 | 19,076 |
| 160 | 853 | 297 | 15,988 | 1,053 | 0·066 | 0·936 | 0·8 | 19,984 |
| 170 | 883 | 272 | 14,593 | 1,254 | 0·086 | 0·914 | 1·1 | 13,265 |
| 180 | 1,433 | 266 | 14,271 | 2,204 | 0·154 | 0·846 | 1·6 | 8,917 |
| 190 | 836 | 241 | 12,983 | 796 | 0·061 | 0·939 | 0·6 | 21,637 |
| 200 | 763 | 209 | 11,367 | 782 | 0·069 | 0·931 | 0·9 | 12,629 |

egg-production is accounted for. This has been demonstrated also by Maclagan[10] from Chapman's own data:

| | | | | | | |
|---|---|---|---|---|---|---|
| Beetles per gramme flour . | 2 | 4 | 8 | 16 | 32 | 64 |
| Eggs per beetle-day . . | 1·56 | 3·80 | 3·00 | 1·56 | 1·04 | 0·80 |

In *Tribolium* as well as in *Drosophila* there exists a clear correlation between population density and fertility. Below and above the optimal density fertility is reduced and the potential fertility is not realized owing to population pressure. This factor accounts no doubt for the largest part of the unrealized potential increase. It is of great interest to gather, again, from this analysis that environmental resistance as well as intensity of struggle for existence do not increase indefinitely, but remain fluctuating at values below saturation. After the population peak is passed, both factors tend to relax, as a rule.

Analysis of research on *Tribolium* shows again how careful one should be in applying a simplified mathematical analysis to rather complex biological phenomena. Stanley treated the given facts successfully as an indefinite periodic fluctuation between predator and prey, applying formulae of chance meeting of gas molecules. The actual analysis shows that this conception is rather incomplete and fails to explain many important numerical features. But it suggests that the biotic factors of population control, to which belong the population density as well as the food relation, are interchangeable in their effect and may possibly be treated successfully by mathematical analysis as one compound factor.

The analysis of the population trend of the honey-bee reveals another type of population growth. Reproduction is here independent of the number of adults produced, as one reproducing female only is to be found within each hive. Extrinsic conditions, as abundance of nectar and pollen, climate and empty space for brood-rearing, act as limitations of the potential increase. As 3,000 eggs laid was the observed maximum for one oviposition day, this has been regarded as the potential increase. Table IX contains the data and their analysis. Environmental resistance reaches 1·0 in the poor season and realization of potential increase does not surpass 0·4 for a 10-days period even in the most

TABLE IX. *Population trend and analysis in honey-bee populations in a single-walled bee hive at Kiryat Anavim, 1936*

| | *A* | *B* | *C* | *D* | *E* | *F* | *G* | *H* |
|---|---|---|---|---|---|---|---|---|
| *Date* | *Total population* | *Reproducing females* | *Potential increase of population* | *Actual no. of eggs laid per period* | *Realization of potential increase* | *Environmental resistance* | *Rate of growth* | *Intensity of struggle for existence* |
| 1.i. | 11,800 | 1 | 33,000 | 4,975 | 0·150 | 0·850 | 1·6 | 20,618 |
| 11.i. | 16,150 | 1 | 30,000 | 4,780 | 0·159 | 0·841 | 1·4 | 21,421 |
| 21.i. | 21,620 | 1 | 30,000 | 5,850 | 0·195 | 0·805 | 1·3 | 23,084 |
| 1.ii. | 27,430 | 1 | 33,000 | 7,065 | 0·214 | 0·786 | 1·3 | 25,384 |
| 11.ii. | 34,545 | 1 | 30,000 | 9,500 | 0·317 | 0·683 | 1·3 | 23,084 |
| 21.ii. | 41,015 | 1 | 30,000 | 9,500 | 0·317 | 0·683 | 1·2 | 24,999 |
| 1.iii. | 48,605 | 1 | 24,000 | 9,940 | 0·413 | 0·587 | 1·2 | 19,999 |
| 11.iii. | 53,935 | 1 | 30,000 | 11,990 | 0·400 | 0·600 | 1·3 | 23,084 |
| 21.iii. | 61,355 | 1 | 30,000 | 9,740 | 0·325 | 0·675 | 1·1 | 27,272 |
| 1.iv. | 65,980 | 1 | 33,000 | 11,375 | 0·345 | 0·655 | 1·1 | 29,999 |
| 11.iv. | 65,325 | 1 | 30,000 | 9,390 | 0·313 | 0·687 | 1·0 | 29,999 |
| 21.iv. | 66,285 | 1 | 30,000 | 9,810 | 0·327 | 0·673 | 1·0 | 29,999 |
| 1.v. | 63,760 | 1 | 30,000 | 9,130 | 0·304 | 0·696 | 1·0 | 29,999 |
| 11.v. | 61,015 | 1 | 30,000 | 9,335 | 0·311 | 0·689 | 1·0 | 29,999 |
| 21.v. | 60,370 | 1 | 30,000 | 9,275 | 0·309 | 0·691 | 1·0 | 29,999 |
| 1.vi. | 57,915 | 1 | 33,000 | 9,320 | 0·282 | 0·718 | 1·0 | 32,999 |
| 11.vi. | 54,015 | 1 | 30,000 | 4,605 | 0·154 | 0·846 | 0·9 | 33,332 |
| 21.vi. | 46,765 | 1 | 30,000 | 4,030 | 0·134 | 0·866 | 0·8 | 37,499 |
| 1.vii. | 42,895 | 1 | 30,000 | 5,075 | 0·167 | 0·833 | 0·9 | 33,332 |
| 11.vii. | 29,230 | 1 | 30,000 | 5,570 | 0·186 | 0·814 | 0·7 | 42,856 |
| 21.vii. | 31,815 | 1 | 30,000 | 5,685 | 0·189 | 0·811 | 1·1 | 27,272 |
| 1.viii. | 32,660 | 1 | 33,000 | 7,570 | 0·229 | 0·771 | 1·0 | 32,999 |
| 11.viii. | 35,135 | 1 | 30,000 | 6,355 | 0·212 | 0·788 | 1·1 | 27,272 |
| 21.viii. | 36,990 | 1 | 30,000 | 6,110 | 0·204 | 0·796 | 1·1 | 27,272 |
| 1.ix. | 37,855 | 1 | 33,000 | 5,925 | 0·198 | 0·802 | 1·0 | 32,999 |
| 11.ix. | 37,690 | 1 | 30,000 | 5,170 | 0·172 | 0·828 | 1·0 | 29,999 |
| 21.ix. | 35,005 | 1 | 30,000 | 4,575 | 0·158 | 0·842 | 0·9 | 33,332 |
| 1.x. | 32,875 | 1 | 30,000 | 4,365 | 0·146 | 0·854 | 0·9 | 33,332 |
| 11.x. | 31,175 | 1 | 30,000 | 3,990 | 0·133 | 0·867 | 1·0 | 29,999 |
| 21.x. | 27,665 | 1 | 30,000 | 3,195 | 0·107 | 0·893 | 0·9 | 33,332 |
| 1.xi. | 23,070 | 1 | 33,000 | 0 | 0·000 | 1·000 | 0·8 | 41,249 |
| 11.xi. | 17,270 | 1 | 30,000 | 1,100 | 0·037 | 0·963 | 0·8 | 37,499 |
| 21.xi. | 14,560 | 1 | 30,000 | 1,320 | 0·044 | 0·956 | 0·8 | 37,499 |
| 1.xii. | 11,895 | 1 | 30,000 | 1,630 | 0·054 | 0·946 | 0·8 | 37,499 |
| 11.xii. | 10,005 | 1 | 30,000 | 1,270 | 0·042 | 0·958 | 0·8 | 37,499 |
| 21.xii. | 7,345 | 1 | 30,000 | 1,630 | 0·054 | 0·946 | 0·7 | 42,856 |

favourable season. The last column, illustrating intensity of struggle for existence, shows that the absolute values are of no importance. It shows the resistance which the queen meets in oviposition. For further analysis the reader is referred to a recent paper of the author.[7]

We are far from having explained the dynamics of the population trend within the *Drosophila* bottle, but the complete population count has raised many new problems and shows the facts from another angle. The experimentation is only at its beginning, but a few facts of outstanding importance may be pointed out:

1. The number of adults hatching is only a fraction of the eggs laid.
2. A prolongation of development is to be expected in the later stages of the culture.
3. Heavy adult hatching occurs just at the final stage, followed by death even before maturity is reached.
4. The final contraction is due to intoxication.
5. Age structure shifts in the same way as that in changing populations of man or honey-bee.
6. Intensity of struggle for existence, as conceived by us, does not grow indefinitely. After development has passed the population peak it decreases or remains constant. An increase in environmental resistance indicates that other factors, besides population pressure, participate in the resistance. (See note f, p. 180.)

# IV

# BIOLOGICAL EQUILIBRIUM IN NATURE AND BIOLOGICAL CONTROL

## I. THE CASE FOR BIOLOGICAL EQUILIBRIUM

THE role biotic factors play is one of the main problems of ecology. Whereas food, population density, diseases, and the reaction basis of the organism belong to the biotic factors as well, we shall discuss first the influence which enemies have upon their host or prey.

In the first period of our knowledge enemies were regarded as the primary factor regulating animal populations. This opinion has found its classical expression with regard to insects in the report of Howard and Fiske[1] on the importation of the parasites of the gipsy-moth and the brown-tail moth into the United States:

> 'To put it dogmatically, each species of insect in a country where the conditions are settled is subjected to a certain fixed average percentage of parasitism which in the vast majority of instances and in connection with numerous other controlling agencies, results in the maintenance of a perfect balance. The insect neither increases to such abundance as to be affected by disease or checked from further multiplication through lack of food, nor does it become extinct, but throughout maintains a degree of abundance in relation to other species existing in the same vicinity, which, when averaged for a long series of years, is constant.
>
> 'In order that this balance may exist it is necessary that among the factors which work together in restricting the multiplication of the species there shall be at least one, if not more, which is what is here termed facultative, and which, by exerting a restraining influence which is relatively more effective when other conditions favour undue increase, serves to prevent it.
>
> 'A very large proportion of the controlling agencies, such as the destruction . . . by (extreme) climatic conditions, is to be classed as catastrophic, since they are wholly independent in their activities upon whether the insect which incidentally suffers is rare or abundant. The average percentage of destruction remains the same, no matter how abundant or how near to extinction the insect may have become.
>
> 'Destruction through . . . birds and other predators, works in a radically different manner. These predators are not directly affected

by the abundance or scarcity of any single item in their varied menu. Like all other creatures they are forced to maintain relatively constant abundance among the other forms of animal and plant life, and since their abundance from year to year is not influenced by the abundance or scarcity of any particular . . . prey they cannot be ranked as elements in the facultative control of such species. On the contrary, they average to destroy a certain gross number of individuals each year, and since this destruction is either constant, or, if variable, is not correlated in its variations to the fluctuations in abundance of the insect preyed upon, it would most probably represent a heavier percentage when that insect was scarce than when it is common. . . . A natural balance can only be maintained through the operation of facultative agencies which effect the destruction of a greater proportionate number of individuals as the insect in question increases in abundance. Of these facultative agencies parasitism appears to be the most subtle in its action. Disease . . . or insufficient food supply does not as a rule become effective until the insect has increased to far beyond its average abundance.'

This is the classical *plaidoyer* for biological equilibrium.

### 2. THE CASE FOR CLIMATIC CONTROL

The conceptions just described dominated the last decades of ecological thought, and only recently a reaction set in, stressing the fact that abiotic factors, principally climate, regulate the numbers of individuals. Long series of observations, mainly on insects, showed an unexpected degree of parallelism between fluctuations of certain climatic factors as temperature, precipitation, humidity, &c., and those of many animal species. Similar fluctuations are observed in such insects and other animals among which enemies and diseases certainly do not play an important role at any period of the gradation.* Moreover, it has been demonstrated by introducing physiological laboratory methods of research that climatic factors, especially temperature and humidity, exert a dominating influence on the vitality of poikilothermous animals at least, and that such processes as fertility, egg-production, longevity, &c., are influenced even by relatively small deviations from the optimal combinations of these factors, the vital optimum. These climatic influences are of dominant importance during certain, generally short, periods of the life-cycle, which are the most sensitive ones.[2]

---

* In studying animal populations we define a gradation as the interval between one lowest point of the population ebb and the next, thus including one full wave of the fluctuation,

Statistical analysis of gradations showed that, as a rule, the share of climatic destruction is much larger than that of all other components, and it was therefore concluded that climate is the main regulator of numeric abundance.

These conclusions have been well represented by Uvarov:[3]

> 'The theory that all living organisms are in a stable equilibrium so far as their relative numbers are concerned is widely recognized to-day. It is however in direct contradiction to the facts. While it is true that an increase in numbers of a species is usually only temporary, and that a decrease will, sooner or later, follow, there are no proofs that the fluctuations in the two directions are of an approximately equal magnitude, as in the case of a pendulum. Nor is the so-called normal number a constant....
>
> 'The theory of stable equilibrium is based on the assumption that the numbers of an organism depend mainly on the numbers of their enemies and on the quantity of food, i.e. on factors which in their turn are dependent on other organisms. No one will deny the controlling value of these factors, but the evidence collected should go far towards proving that the key to the problem of balance in nature is to be looked for in the influence of climatic factors on living organisms. These factors cause a regular elimination of an enormous percentage of individuals under so-called normal conditions, which in fact are such that insects survive them, not because they are perfectly adapted to them, but only owing to their often fantastically high reproductive abilities. Any temporary deviations in the climatic factors, however slight they may be, affect the percentage of survival, either directly, or indirectly (through natural enemies and food-plants), and thus influence abundance. Further, the ecoclimatic succession and the geological succession of climates favour the survival and the relative abundance of some species, and condemn others to a complete extermination. Of course, the food, the natural enemies, the competition between individuals and between species, all play their part in these evolutionary processes, but none of these factors are independent and primary in character, since they themselves are deeply affected by climate. It is possible to imagine an insect with no natural enemies and without any need to compete for food, shelter, etc., and there is no doubt that this, if not very commonly, does actually happen in nature, but an insect living under natural conditions and yet free from climatic influences is an absurdity.... To study the dynamic balance of a species without taking into consideration its climatic environment, is an utterly unscientific procedure.'

This is the case *in nuce* for the climatic school.

### 3. MATHEMATICAL AND EXPERIMENTAL APPROACH

The problem of intra- as well as interspecific regulation has been approached within the past decade from the experimental as well as from the theoretically mathematical point of view.

The problem of intraspecific regulation has been discussed amply in a previous essay.[4] The logistic growth of the population is the result of given conditions. Within a limited space a population is being more and more forced from an initial exponential growth into a logistic one, by population pressure, i.e. by a factor determined mainly by the reaction basis of the organism itself.

The problem of interspecific regulation has been attacked by theoretical analysis by Volterra[5] and Lotka[6] and experimentally by Gause.[7]

Mathematical analysis must necessarily begin with a simplified hypothesis in order to obtain general conclusions. Volterra based his analysis on the assumption that only the voracity of the predator with regard to a given prey and the reproductive capacity of those species living together were the effective factors, all other conditions being constant. On this basis he arrived at the following fundamental laws governing the fluctuations of two species living together:

'I. *Law of the periodic cycle.* The fluctuations of the two species are periodic and the period depends only upon $\epsilon_1$, $\epsilon_2$, and C (namely upon the coefficients of increase and decrease and the initial conditions.

'II. *Law of the conservation of the averages.* The averages of the numbers of individuals of the two species are constant whatever may be the initial values of the numbers of individuals of the two species just so long as the coefficients of increase and decrease of the two species and those of protection and of offence ($\epsilon_1$, $\epsilon_2$, $\gamma_1$, $\gamma_2$) remain constant.

'III. *Law of the disturbance of the averages.* If an attempt is made to destroy the individuals of the two species uniformly and in proportion to their number, the average of the number of individuals of the species that is eaten increases, and that of the individuals of the species feeding upon the other diminishes. Increase of the protection of the species fed upon increases, however, both the averages.'[5a]

Other types of 'associations' as well as many special cases have been discussed. However, of fundamental importance is the fact that Volterra and his followers obtained fluctuations, based on the above-mentioned assumptions, which are strictly in accordance with the theory of Howard and Fiske (Fig. 15).

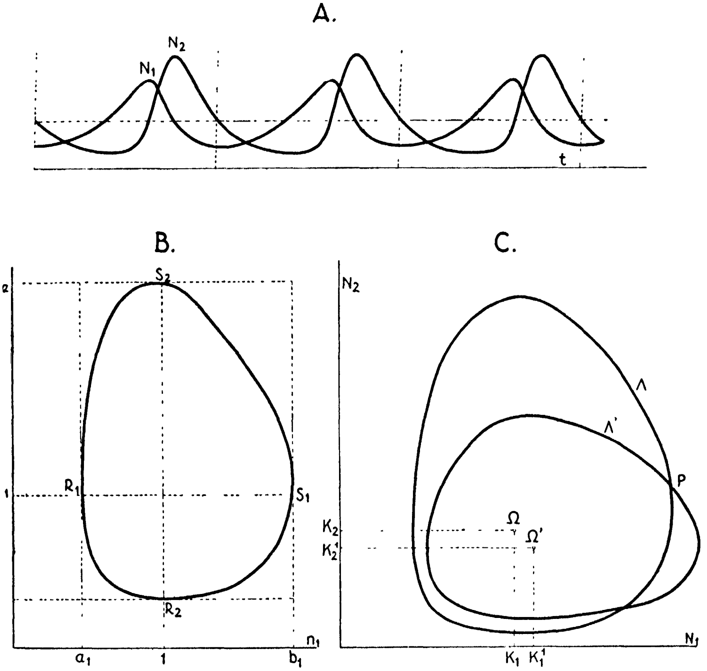


FIG. 15. A. Fluctuations of two species, one of which devours the other.
B. Diagram of numerical variation in two species, one of which devours the other. Each point of the cycle gives the numbers of the predator and the prey living at a given moment.
C. Diagram of the change of cyclic fluctuation, when both species are uniformly and proportionally destroyed. (After Volterra.)

Experiments on interspecific influence of population growth have only recently been made and mathematically analysed by Gause. Some extremely illuminating cases may be summarized:

1. Two species competing in identical niches. Fig. 16, A, shows the separate growth of two ciliates under identical conditions within a test-tube. One species, *Glaucoma scintillans*, fits better into the environment, and in concordance with

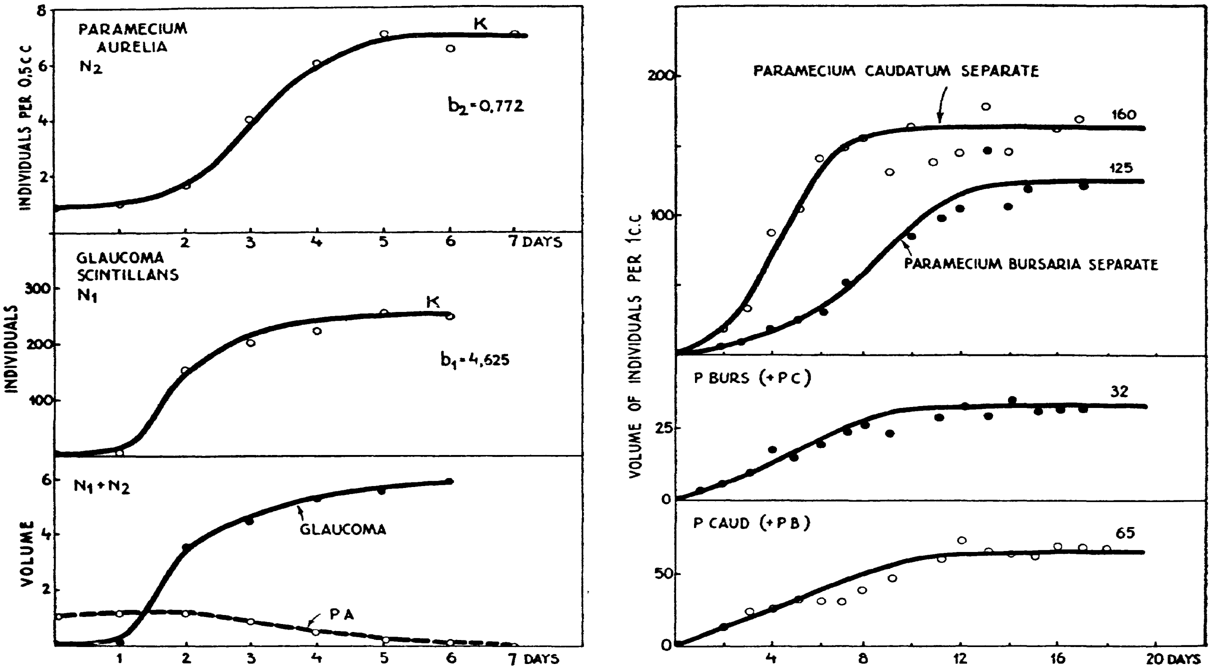


FIG. 16. Interspecific competition. Left: between species of identical niches. Right: between species of different niches but identical food. (After Gause.)

Volterra's calculations the second species, *Paramaecium caudatum*, is expelled finally from this environment, if both grow in a mixed culture.

2. Two species of different niches, but in competition of the same food. Fig. 16,B, illustrates this case for *Paramaecium caudatum* and *P. bursaria*, fed on *Saccharomyces exiguus* and *Bacillus pyocyaneus*. Each species having the advantage of its proper niche, both species may coexist for an infinite period, which result is again in agreement with mathematical analysis.

3. Two species, one of which feeds on the second. Fig. 17 shows the consequence of the introduction of the predatory *Didinium nasutum* within a population of its prey *Paramaecium caudatum*. The possibilities are more complex than in the earlier-mentioned cases. If the test-tube is without oat-sediment, the predator destroys its host in this extremely simple and limited environment fully, and has to die from starvation in consequence (Fig. 17, A, *a*). But when this microhabitat contains a refuge for the prey, e.g. in form of an oat sediment, and if *Paramaecium* and *Didinium* are simultaneously introduced into the microhabitat, the number of predators increases somewhat and they devour a certain number of *Paramaecia*, but a considerable amount of the prey is in the refuge and the predators cannot attain it. Finally, the predators die out entirely owing to lack of food, and then an intense multiplication of the paramaecia (no cysts of *Didinium* being observed) begins in the microcosm (Fig. 17, A, *b*). An experiment under more complex conditions and more in conformity with natural conditions, showed the effect of regular immigrations of a predator into an environment with refuge (Fig. 17, A, *c*). At the first immigration the test-tube contained a few *Paramaecia* only, the predator died by starvation and the prey began to increase considerably. The second immigration met with a higher population level of the prey. *Didinium* increased considerably and *Paramaecium* was greatly reduced. The third immigration occurred at the population peak of *Didinium* and did not cause any essential changes. At the time of the fourth immigration the predator had already devoured all the prey, had become reduced in size and degenerated. The prey was

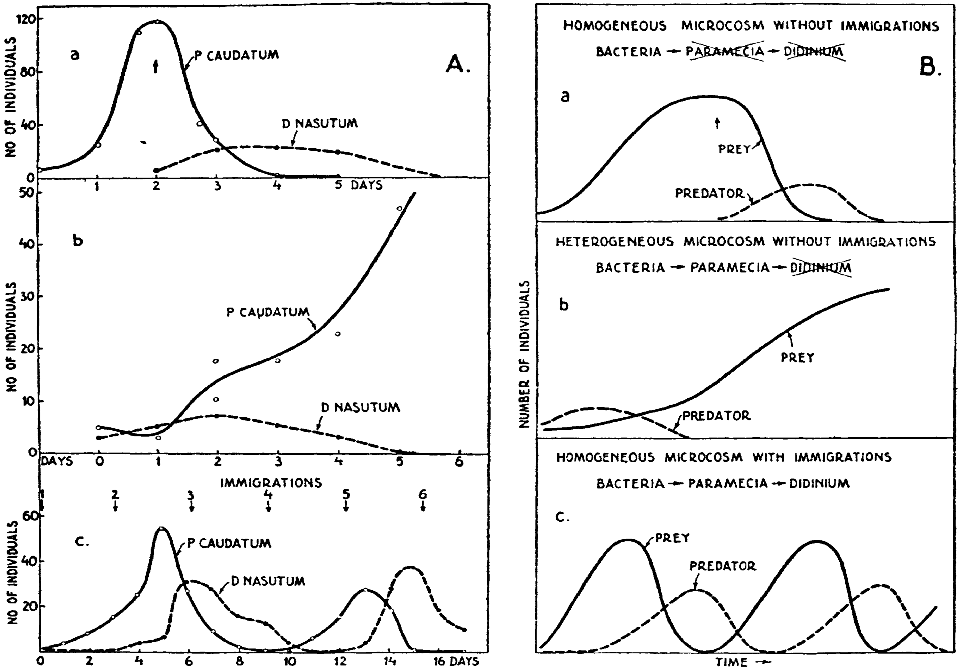


FIG. 17. Interaction of populations of two species, one of which (*Didinium*) preys on the other (*Paramaecium*). A. Experimental result. B. Schematic curves. (After Gause.)

now introduced into the test-tube, and a new cycle of growth of the prey population originated. Such periodic changes repeat themselves farther on. All these eventualities are supported by mathematical analysis.

Similar experimental results have been obtained by mixed populations of the flour mite *Aleuroglyphus agilis* and its predator *Cheyletus eruditus*.[7]

The most interesting result of these experiments is that the classical uninterrupted fluctuations are restricted to cases where the devouring power of the predator is limited or submitted to the laws of chance. But when the devouring power of the predatory population is high in a limited and simple environment without efficient specific refuges for the prey, it will end in destruction of both species. But when an interrupted or permanent immigration of individuals of both species, the predator as well as the prey, exists, another phenomenon takes place, called by Gause relaxation-oscillations. It is easily symbolized by the oscillations of the water surface in Tantale's vessel.

> 'Into a water tank enters an uninterrupted flow of water, analogue to our immigrations. When the water surface attains the level *H*, a siphon begins to work (= period of growth of predatory population) and the tank empties itself rapidly until the level of *h*. Then, the cycle repeats itself from the beginning. In this system of auto-oscillation we have consequently a source of constant energy, a critical threshold and a specific part which fluctuates.'

If the protective power of the prey is subsequently also raised, the fluctuation returns from the relaxation type to the classical oscillations.

These and other recent experiments have shown quite clearly that under proper conditions the theoretical analysis of Volterra, Lotka, and others can be verified and realized. The question remains as to what extent such demonstrations made under constant conditions with a limited and extremely simplified space may be transferred into nature. It is still premature to pronounce a judgement in this respect. Continuous change of other environmental factors will certainly interfere with the verification of the ideal curves obtained in the laboratory. Fluctuations of the relaxation types have been observed in nature. To this type belongs the shift of the lady-beetle *Novius cardinalis* to other microcentres of *Icerya* increase within the same citrus-orchard, as soon as the density of *I. purchasi* has declined below a certain minimal threshold of maintenance necessary for mass development of *Novius*.[8]

Considering, however, the complexity of the phenomenon of animal fluctuations in nature it seems premature to apply the formulae of Volterra to actual fluctuations observed. What basic mistakes may originate from such applications may be gathered from one very illuminating case. Volterra's interest was aroused mainly by an interview with d'Ancona, who observed that after interruption of the fisheries in the Adriatic during the last war the percentage of selachians, i.e. of the main predators among the benthal fauna, rose greatly and declined parallel with the beginning of fishery after the war. This case induced Volterra to attempt a mathematical analysis, and found its solution in the third law of fluctuation quoted above.[9] A complementary study made by the present author showed definitely that three such fluctuations of approximately equal size were observed between 1900 and 1930, and that the parallelism between interruption of fishery and increased percentage of selachians is doubtless only a chance one.[10] Fluctuations of hydrographical factors are probably responsible for them. The application of Volterra's formulae to natural fluctuations seems still premature. This does not decrease the intrinsic value of these studies, which have been corroborated under laboratory conditions. A long time will pass before they are fit for application to and explanation of phenomena observed in nature on a larger scale.

## 4. ANALYSIS OF RECENTLY PUBLISHED FACTS ON BIOLOGICAL EQUILIBRIUM

Where is the evidence that parasites correspond to the fluctuations of their host? In the great majority of the parasites with which the author became acquainted during his own experience an abundant food-supply is a *conditio sine qua non* for their own mass-appearance. Every student of nature well knows that the abundance of parasites in forest-insects, for example, or in scale-insects, aphids, &c., is observed only at the peak of the host's seasonal fluctuation or gradation. The question arises as to whether the differentiation proposed by Howard and Fiske[1] that diseases and food-limitation work differently from the parasites because they appear only as a consequence of the host's mass-increase, and therefore cannot prevent the increase, is really justified. Is there any conclusive proof or indication that parasites react in their numerical fluctuations to those of the host which precede its increase? Or does the parasite's increase only follow that of the host after the latter has surpassed a certain threshold, thus limiting it to a certain degree just at its population peak, when other environmental resistances, as population density, diseases, &c., and, eventually, unfavourable climatic conditions begin to have a reducing effect anyhow? Such is clearly the case in red scale and *Chilocorus bipustulatus*, in aphids and Chalcidids, and in voles and their predators in Palestine.

Most of these questions will be definitely answered only after more statistical and observational material has been accumulated. It may be assumed, however, in view of present-day experience, that the answers will not always agree with Howard's theory.

Biotic factors are most conspicuous at the peak of an outbreak and when the outbreak begins to decrease.

The first biotic factor to be discussed here is the influence of intraspecific population pressure. Pearl's classical experiments regarding growth of *Drosophila* populations within the milk bottle have appeared repeatedly in recent discussions.[11] It will therefore be useful to quote some of our recent experiences of what really occurs within this bottle.[12]

The upper asymptote of a stable population at the saturation point is thus clearly determined by the interaction of influence of physical and physiological capacity of the environment as well as by changes in the vitality and fertility itself brought on by population density. Again, the experiments of Chapman[13] and Holdaway[14] with *Tribolium*-populations at different conditions of temperature, humidity, and food-quantity illustrate this point. The question remains as to how far these laboratory results gained with insects living under constant conditions and *in a limited space* may be applied to natural phenomena. It is apparent that all those animals which do not live in a saturated environment, i.e. whose population is depressed below the theoretical environmental capacity by climatic factors or by behaviour incompletely adapted to their present environment, &c., are not concerned by these experiments. The same is correct for animals which normally fluctuate heavily in number in the interval between the gradations. But there is little doubt that intraspecific population pressure is often a very important point at the peak of the outbreak. In most animals hitherto studied a reduction in size, fertility, and vitality is induced by this pressure when it has passed the local maximum capacity for the specific stable population. In other animals, it leads to changes of behaviour ending in large migrations (locusts, lemmings, &c.). In other animals again, as in many birds, the choice and maintenance of a breeding territory prevents the appearance of any overpopulation *a priori* by denying reproduction to the surplus.[15] Also, in those animals which live more or less permanently in a saturated environment in-

TABLE I. *Influence of age of culture and population density on some vital processes of* Drosophila

| *Age of culture in days* | *No. of females* | *Longevity of females hatched that day* | *No. of eggs laid per female* | *Age of culture in days* | *No. of females* | *Longevity of females hatched that day* | *No. of eggs laid per female* |
|---|---|---|---|---|---|---|---|
| 1 | 2 | 13·0 | .. | 16 | 98 | 9·0 | 1·0 |
| 2 | 2 | .. | 8 | 17 | 74 | 8·0 | 0·50 |
| 3 | 2 | .. | 46 | 18 | 125 | 8·8 | 0·25 |
| 4 | 2 | .. | 65 | 19 | 103 | 9·7 | 0·50 |
| 5 | 2 | .. | 70 | 20 | 116 | 9·0 | 0·50 |
| 6 | 2 | .. | 40 | 21 | 124 | 8·0 | 2·0 |
| 7 | 2 | .. | 33 | 22 | 85 | 7·0 | 0·9 |
| 8 | 2 | .. | 16 | 23 | 92 | 6·0 | 0·7 |
| 9 | 2 | .. | 12 | 24 | 62 | 5·0 | .. |
| 10 | 2 | .. | 3 | 25 | 56 | 4·0 | 0·1 |
| 11 | 15 | 5·1 | 5 | 26 | 57 | 3·0 | 0·2 |
| 12 | 63 | 9·4 | 2 | 27 | 65 | 2·0 | 0·2 |
| 13 | 74 | 11·0 | 1·2 | 28 | 59 | 1·0 | 0·8 |
| 14 | 94 | 10·0 | 2·0 | 29 | 30 | 0·43 | 0·0 |
| 15 | 114 | 9·9 | 2·7 | 30 | 27 | 0·39 | 0·2 |

crease means introduction of unfavourable environmental conditions and lowering of vitality. In such insects as blow-flies and other carrion flies, where there is, as a rule, a surplus of adults in the population, increase of flies does not mean increased offspring, because the limiting factor of suitable carrion present is not changed and maximal oviposition on all carrion is guaranteed, as a rule, by the normal number of flies.

The interaction of abiotic and biotic environmental factors as well as the physiological reaction of the organism create the conception of vital capacity of the habitat towards any animal. This 'saturated' state following the actual filling of this local vital capacity may scarcely be regarded as an equilibrium maintained by oscillations. It is rather the result of the clash between the actual expansive tendency of the organism concerned and the restricting effect of the environment. Every organism tends to fill its environment until the saturation point has been reached. Really saturated populations are, however, not the rule in nature, where temporary effective factors reduce the population below this point generation after generation. In these cases intraspecific population pressure has no importance whatsoever. This is correct for the majority of insect pests or rodents, for example, as long as they are not on the increasing wave of a gradation. A misconception often heard in this connexion is the opinion that it is possible to stop environmental saturation, which always follows a logistic curve in its growth, half-way through. A school of thought exists among scientists dealing with human populations, mainly in the Anglo-Saxon countries, which claims that it is possible to fix human populations at the individual optimum, the turning-point of the logistic curve.[16] Development always tends, and probably will tend, to reach the upper asymptote, the stable maximum, where conditions are decidedly not optimal to the individual, with greatest biological speed.

We shall now proceed to analyse a few cases of critical years in gradations, i.e. those years which end gradations, and again we choose our examples from forest insects in central Europe and from horticultural pests in Palestine.

For *Panolis flammea* we possess satisfactory observations on the crises of the two last gradations in north Germany. The first gradation ended in the following way:[17]

| | | *No. of individuals lacking or destroyed* |
|---|---|---|
| No. of eggs to be expected per tree (from 17·4 moths) | 1,200 | |
| No. of eggs actually laid | 250 | 950 |
| Egg mortality (20% *Trichogramma*+20% non-hatching eggs) | 150 | 100 |
| Neonate caterpillar (until June 99·3% by climate and constitution) | 1·100 | 148·9 |
| Old caterpillar (78·9% parasites+7·7% diverse) | 0·05 | 1·05 |
| Pupa (16·4 parasites+14·1 diverse) | 0·032 | 0·018 |
| Moths hatched per tree | 0·0043 | 0·0297 |

The reaction of this generation to the parent generation is 0·004 : 14·4, or 1 : 7,350. If only climatic factors had been effective 0·9 moths would have hatched and if only enemies, 35. This gives a proportion of 1 : 39 in favour of the climatic and constitutional factors, into which the effect of strong intraspecific population pressure is possibly included.

The crisis in the following gradation occurred as follows:[18]

| | | *No. of individuals lacking or destroyed* |
|---|---|---|
| No. of pupae per sq. m. | 100 (relative) | |
| Pupal mortality (59% predators+17% diseases +1% various) | 33·6 | 66·4 |
| Moth mortality (53% weather+16% predators) | 13·3 | 20·3 |
| Eggs laid | 792 | |
| Egg mortality (10·4% climate+1·4% enemies +1% unfertilized) | 690·6 | 101·4 |
| Caterpillar first stage (16% climate+8% hunger +9% predators) | 490·2 | 200·4 |
| Caterpillar later stages (18+18+46+70% enemies and diseases) | 50·7 | 439·5 |
| During pupation (99% parasites) | 0·5 | 50·2 |

In this case the reduction was 1 : 200, but the destructive power of enemies was 632 times higher than that of the climate, which alone would have reduced the population to 326 pupae only in the next generation. The influence of climate and intraspecific population pressure on the number of eggs laid is omitted in this calculation.

In the year preceding this crisis the number of pupae per sq. m. in a certain area increased from 30 to 50·9.[19] In this year climatic reduction alone was responsible for a reduction from 522·6 eggs per sq. m. to 130·8, the difference being ascribed to enemies.

The last gradation of *Dendrolimus pini* ended:[20]

| | | *No. of individuals lacking or destroyed* |
|---|---|---|
| Hibernating caterpillars per tree . . . . | 444 | .. |
| Hibernating caterpillars (3% parasites+10% climate+18% predators and hunger) . . | 41 | 403 |
| Pupal mortality (17% consequence of hunger+20% parasites+8% birds) . . . | 23 | 18 |
| Moths (theoretical egg production) . . . | 1,496 | .. |
| Moths (destruction and prenatal mortality 77%, eggs remain) . . . . . . . . | 346 | 1,150 |
| Egg mortality (6% enemies+8% unfertilized+36% 'constitution') . . . . . | 173 | 173 |
| Young caterpillars mortality (77% climate and constitution+9% enemies and diseases) . | 24 | 149 |

Analysing this development we find that each of the three major factors, if working alone, would have reduced 444 hibernating caterpillars until hatching of the moth as follows:

Enemies and diseases to 184 individuals
Lack of food „ 225 „
Climate „ 400 „

The picture presented during the period from hatching of moth to hibernation is different when climatic and 'constitutional' factors working alone would have reduced the 1,496 eggs to 29 caterpillars. But in the following period, enemies and diseases alone would have killed, until the hatching of the moth, 25·8 out of those 29 caterpillars, climate alone only 2·9.

Schwerdtfeger gives a fair summary of the observed facts:

> 'In all stages and ages *Dendrolimus* has died in varying quantity. Destructive factors of all kinds have permanently co-operated sometimes in higher, sometimes in a lower degree on the diminution of the *Dendrolimus* population. It is impossible to say that the calamity has

broken down through *one* cause, e.g. parasites or unfavourable weather conditions. A long sequence of factors, some of which were of greater, others of less importance, have interacted in order to bring about the collapse of this outbreak.'[20]

This is true for all analyses given above.

These results would, however, be misleading should the conclusion be drawn that biotic factors always play a highly important role. The author can quote quite a few cases of mass outbreaks from his own limited experience where the share of enemies in the crisis was negligible.

In spring 1926 an outstanding outbreak of the vine hawk moth *Chaerocampa celerio* occurred throughout the vine-growing districts of Palestine.[21] The following generation disappeared almost totally from the vineyards, whereas in our breedings only 15 per cent. of the eggs of the 1st generation and 5 per cent. of the 2nd generation hatched. No diseases were observed, and parasites as well as predators have certainly remained below 2–3 per cent. on the general average.

The almond sawfly *Cimbex humeralis* was in gradation for a series of years at Hartov (1923–6).[22] The caterpillars were refused by predators, and the maximum average parasitism during the peak of the outbreak was 10–15 per cent.

The last two outbreaks of the desert locust *Schistocerca gregaria*[23] in the Sudan-Palestine cycle broke down due to the delay in prevailing winds at the normal season for re-migration to the Sudan and also to drought in the oviposition season.

A more recent discussion of locust populations in general also shows that, although locusts are a staple food of natural enemies in years of outbreaks, the latter's share in breaking a gradation is small and unreliable. Epidemics which may break out only during gradations are entirely dependent upon favourable climatic conditions.[24]

Again, in citrus-scales, where almost annually one or the other coccid is in gradation in groves of a certain age towards autumn and winter, the biotic component in the crisis is almost negligible.[25] If this is true for the red scale (*Aonidiella aurantii*), it is certainly correct for the mussel scale (*Mytilococcus beckii*) where even the small amount of parasitism observed in the red scale is absent.

The role parasites play may be approached from still another angle. If parasitism is the regulating factor in animal abundance, superparasitism should logically be the primary controlling factor in parasites. Superparasitism should either be effective in reducing and retarding the effect of primary parasitism in a very efficient manner or, if not, it puts into doubt the regulatory value of parasitism itself.

A few actual cases may be reported:

Parasites do little damage to the lac crops, and hyperparasites are of little value as controlling agents of parasites of *Laccifer lacca* Kerr.[26]

| | *Parasites* | | *Hyperparasites* | |
|---|---|---|---|---|
| *Year* | *Host cells present* | *Average % of parasites* | *Hosts present* | *Average % of hyperparasites* |
| 1928/9 | 14,638 | 3·4 | . . | . . |
| 1929/30 | 42,386 | 4·7 | 1,078 | 0·9 |
| 1930/1 | 72,772 | 2·6 | 1,764 | 0·4 |
| 1931/2 | 61,879 | 4·2 | 4,381 | 8·6 |
| 1932/3 | 121,238 | 7·2 | 14,202 | 3·4 |
| 1933/4 | 138,878 | 5·7 | 10,560 | 1·6 |
| 1934/5 | 117,679 | 6·1 | 10,131 | 4·0 |
| Average | . . | 5·1 | . . | 3·2 |

In the open nests of the apple-web moth *Hyponomeuta malinella* in Yugoslavia, where parasitism is fairly low, superparasitism on the most important primary parasite *Angitia armillata* is often considerable:[27]

| *Parasites on* | *Nest 1* | *Nest 2* | *Nest 3* | *Nest 4* | *Average* |
|---|---|---|---|---|---|
| *Hyponomeuta* | 17 | 22 | 21 | 2 | 16% |
| *Angitia* | 30 | 39 | 59 | 29 | 37% |

In the case of *Apanteles melanoscelus*, a valuable primary parasite of the gypsy moth,[28] secondary parasites seem to be of the greatest importance. The superparasites are in general much less discriminating with regard to host selection than primary parasites. Adult secondaries often puncture holes in primary parasites for the sole purpose of feeding on them, and this is no doubt responsible for a great amount of destruction of primary parasites, combining thus the benefits of parasitism and predation. The 35 species of superparasites indicate that 25 to 30 per cent. of the 1st generation's cocoons of *Apanteles* produce adults, while less than 1 per cent. of the 2-generation cocoons, carrying the species over winter, produce primary adults the following spring. Fifty per cent. or more of these cocoons yield neither primaries nor secondaries, as a result of feeding punctures, of strenuous competition, of climate, and of tertiary parasites. However, this case is isolated in its high degree of superparasitism.

Strong competition is intra- as well as interspecifically an important limiting factor, as has been found in Hawaii with regard to parasites of *Ceratitis capitata*.[29]

### 5. ARGUMENTS ARISING FROM RECENT DISCUSSIONS ON BIOLOGICAL EQUILIBRIUM

The main point in many recent discussions is the differentiation between density-dependent and density-independent factors. The theory is promoted that only density-dependent factors (as parasites) are able to regulate animal populations, whereas density-independent factors (as climate) may only destroy. This conception was first promoted by Howard and Fiske[1] and forms the main topic of the papers published by Smith[32] and Nicholson.[33] This discussion is based essentially on an ambiguous definition of terms.

The only reasonable definition of population density seems to refer to the number of individuals present in a unit area. This definition accepted, Kirkpatrick's[34] conclusion is correct:

> 'The fallacy appears to lie chiefly in the confusion between control of density by balance (for which it is true that "the action of the controlling factor must be governed by the density of the population controlled") and control in the ordinary sense of the word, i.e. reduction of the density, which can be equally well affected by factors, such as climate, which are in no way governed by the density of the population.'

Assuming that the conception of the biological school is correct, no technical control by spraying, fumigation, &c., would be justified, as it certainly belongs to the density-independent group. The fact that technical control has the greatest influence on the number of the controlled species contradicts the above-mentioned statement.

Another conception needing clearance is 'regulation'. Regulation may mean the effect of an intrinsic regulator of a biological equilibrium, or it may simply mean the release of a part on an electrical switchboard, determining intensity of work and resistance or direction within a machine. In this essay, it is always used in the second sense.

A very basic theory of the 'biological' school claims that an insect increases rapidly in number after having been introduced into a new environment, because the native enemies of this insect have not been introduced and the enemy-component is therefore absent or entirely insufficient.

Handschin[35] has recently shown that parasites of the Buffalo-fly, *Lyperosia exigua*, are extremely rare at Java, its native habitat, and had to be bred from other Muscids, before *Lyperosia* could be infested. In Australia, however, where the water buffalo was only recently introduced, Australian parasites are common in *L. exigua*. This shows that the abundance of the fly in Australia is not due to absence of the enemies in the native habitat.

The European corn-borer (*Pyrausta nubilalis*) has recently been introduced into North America, where it has developed to a major pest and has spread with great rapidity over the corn-cultivated area. Its enemies there have been hitherto decidedly negligible (except for human agency), and the most competent conclusion with regard to its status is:[36]

> 'It has been demonstrated that corn borer abundance can be correlated with climate and weather, vegetation types and soil types; it can be correlated with soil fertility and cultural practices, such as date of planting, variety, kind of rotation, time of plowing and fertilizer application; and, more significantly still, it can be correlated with the quantity and quality of corn at the period of moth flight.'

Again, for the native habitat of *P. nubilalis* the most competent observers state[37] that no definite correlation has been observed 'between the quantitative or qualitative composition of the fauna parasitic on the borer and the degree of infestation or extent of damage observed in the various zones. Areas in which parasitism is high are not necessarily those in which *Pyrausta* is least injurious' and vice versa. The average total parasitism fluctuates in central and southern Europe between 10 and 36 per cent.[38] However, this parasitism works only after a 90 per cent. mortality, due to climatic or host resistance, has been passed. The main point seems to have been missed by most students: the change of environment has enormously increased the vitality and the euryoecy of the species in North America. Thanks to the thorough research made by the American entomologists, we are able to express this change in figures:[39] whereas *P. nubilalis* has been recorded from about 12 hosts in its native habitat, only 1 (corn) being a primary host, the same species has invaded in its new habitat over 200 plants, belonging to 40 different families. Thirty-five plants are definitely recorded as true hosts; for a large number of the remainder this is highly probable, many of them being primary hosts. This sudden polyphagic development is, as has been shown by the author,[40] a definite indicator of increased general vigour and greater vitality(g). The primary reason for the abundance in the new environment is, hence, a physiological reconstruction within the insect stimulated by the new environment, and probably —our knowledge of such phenomena still being at its beginning—decreasing slowly with time.

A similar explanation may partly illustrate the rapid spread of European sparrows and starlings in North America. But in this case the introduced species were certainly more euryoecous (ecologically plastic) from the start than their native competitors.

One of the species which Howard and Fiske[1] had in mind was the gipsy moth (*Lymantria dispar*). It is of greatest interest to note that Komarek[41] has come to the conclusion, after many years of study of the moth in its native and natural habitat, that the climatic resistance of all stages of development of Tachinid flies is lower than that of the gipsy moth. Hymenopterous parasites are still less important and certainly have no regulatory influence at all on the host population.

These few cases chosen from comprehensive and equally conclusive material show, again, that parasites are often a secondary factor in regulating animal populations in their native home and that other factors, as vitality changes in the

(g) See note g, p. 180.

organism, are, as a rule, of greater importance than the lack of a few parasites or other enemies.

One very basic misconception appeared in recent discussions. The authors agree that climatic or other density-independent factors may destroy a very high percentage of every generation. But even if, for example, 98 per cent. of the offspring were killed by climatic factors and 99 per cent. destruction was needed for the maintenance of the same number of individuals within the next generation, there would be a permanent increase of population, provided this 1 per cent. of difference is not destroyed by enemies. They pretend that climatic factors are for this reason unable to regulate population density or abundance whereas the small percentage killed by enemies does so. That this interpretation gives the true meaning of this school is made clear e.g. by Smith's[32] figure 129. The fallacy is obvious: it is not correct to assume that climatic destruction—important as it may be—is constant, whereas destruction by enemies fluctuates with population density. Climate fluctuates enormously, and its destructive effect on any species changes considerably from generation to generation. This may be illustrated by total resistance of environment of 32 generations of red scale in Palestine, where the enemy component is almost negligible.

TABLE I. *Environmental resistance of* 32 *generations of Red Scale in Palestine*

| *Generation* | *I* | *II* | *III* | *IV* | *Average* |
|---|---|---|---|---|---|
| No. of eggs per female | 100 | 150 | 100 | 50 | .. |
| Resistance ($R_0$), per cent. | 98·00 | 98·67 | 98·00 | 96·00 | .. |
| 1929 | 99·05 | *79·12* | 98·18 | 99·41 | 93·94 |
| 1930 | 93·90 | 98·14 | 98·38 | 99·50 | 97·48 |
| 1931 | 96·00 | 97·71 | 97·81 | 98·79 | 97·58 |
| 1932 | 97·00 | 95·05 | 99·19 | 99·41 | 97·66 |
| 1933 | 97·00 | *98·89* | *92·40* | 97·58 | 96·47 |
| 1934 | *99·38* | 94·68 | 99·13 | *92·00* | *98·30* |
| 1935 | *92·14* | 91·17 | 98·16 | *99·88* | 95·34 |
| 1936 | 98·45 | 93·62 | 98·62 | .. | .. |

With regard to the regulatory value of predators the conception of Howard and Fiske is partly justified. Birds, provided the local bird fauna is regarded as a whole, prey on insects in the degree of their accessibility.[42] This means that, in the end, the same proportion of all species is always eaten and that the absolute food quantity is relatively higher when the species is less abundant than when it is at its peak. In years of exceptional abundance of prey the breeding territory of birds is often reduced or, outside the breeding season, more birds than usual are attracted to the district with exceptionally abundant food-supply. The gathering together of birds of prey in districts of local vole outbreaks illustrates this fact.

Furthermore, there exists a group of catholic predators, some reduviid bugs, carabid beetles, selachians, and cattle-fish, &c., among which the annual or seasonal fluctuations of host abundance exert, as a rule, no influence whatsoever on numerical abundance, for the food present always satisfies their needs. Minor fluctuations may be induced by differential food value of various hosts, but those are mostly superimposed on the major fluctuations dependent on climatic conditions. This is the case in the Indian cotton-bug *Dysdercus cingulatus*, where malvaceous plants abound as food-supply but bug populations are limited by climate.[43]

There exist, however, other predators which compete with the most efficient cases of parasites known. The cases of *Novius cardinalis* versus *Icerya purchasi*[8] and of *Sympherobius amicus* versus *Pseudococcus citri*[44] have been analysed by the author in Palestine. Thompson[45] has reviewed the problem and has demonstrated that there is no basis for the discrimination of predators in favour of parasites, both being probably of equal importance, as good predators are of extremely high destructive value. This agrees fully with our own experiences.

In order to study the question of oscillations around a certain average or equilibrium we must first study the size of those fluctuations. Unfortunately, rather few statistical data, over a sufficiently great number of generations, are at our disposal.

Monthly counts of the Florida wax scale (*Ceroplastes floridensis*) in Palestine, which are rather representative for insects showing a mediocre range of fluctuation in abundance, over 8 years, i.e. over 24 generations, may be compared with parallel counts of the chaff scale (*Parlatoria camelliae*) which represents those insects which show extremely small population fluctuations.

TABLE II. *Eight years population counts of* Ceroplastes floridensis *and of* Parlatoria camelliae (*on* 400 *citrus leaves near Hedera*)

*Ceroplastes floridensis*

| Year | Month<br>i | ii | iii | iv | v | vi | vii | viii | ix | x | xi | xii | Total | Max/Min. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1929 | 118 | 39 | 26 | 12 | 9 | 1,891 | 1,298 | 1,783 | 2,248 | 1,568 | 1,365 | 865 | 11,222 | 270 |
| 1930 | 413 | 375 | 190 | 119 | 325 | *4,420* | 2,546 | 1,566 | 1,069 | 941 | 565 | 318 | 12,801 | 37 |
| 1931 | 239 | 83 | 110 | 72 | 165 | 495 | 355 | 243 | 74 | 158 | 106 | 93 | 2,195 | 7 |
| 1932 | 55 | 34 | 20 | 14 | 15 | 516 | 433 | 209 | 51 | 80 | 103 | 58 | 1,588 | 37 |
| 1933 | 75 | 46 | 18 | 30 | 58 | 206 | 27 | 37 | 33 | 100 | 105 | 109 | 894 | 11 |
| 1934 | 61 | 42 | 24 | *6* | 8 | 68 | 35 | 24 | 53 | 28 | 28 | 20 | 397 | 11 |
| 1935 | 15 | 30 | 50 | 22 | 18 | 22 | 76 | 93 | 53 | 105 | 177 | 132 | 792 | 12 |
| 1936 | 100 | 125 | 104 | 84 | 33 | 149 | 16 | 7 | 16 | 19 | 16 | 15 | 686 | 21 |

Maximum range. 4,420 : 6 = 737

*Parlatoria camelliae*

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1929 | | 121 | | 445 | 379 | 52 | 138 | | 459 | 90 | 155 | 301 | | |
| 1930 | 406 | 532 | *891* | 656 | 561 | 87 | 98 | 45 | 158 | 164 | 288 | 506 | 4,392 | 20 |
| 1931 | 523 | 673 | 588 | 537 | 163 | 55 | 44 | 106 | 151 | 158 | 439 | 286 | 3,723 | 15 |
| 1932 | 502 | 475 | 660 | 705 | 584 | 112 | 42 | 59 | 163 | 273 | 297 | 439 | 4,311 | 17 |
| 1933 | 392 | 472 | 516 | 343 | 267 | 57 | 59 | 84 | 182 | 376 | 322 | 267 | 3,337 | 9 |
| 1934 | 757 | 234 | 407 | 580 | 134 | 61 | 84 | 124 | 101 | 120 | 162 | 271 | 2,835 | 32 |
| 1935 | 293 | 669 | 574 | 605 | 398 | 28 | 67 | 112 | 63 | 198 | 342 | 317 | 3,666 | 24 |
| 1936 | 258 | 189 | 167 | 144 | 69 | 73 | 32 | *6* | 15 | 57 | 54 | 88 | 1,152 | 43 |

Maximum range 891 . 6 = 149.

Ample statistical material of this type will be published soon.[25] Other statistics over long periods are available on forest pests in Germany. These data have been ably analysed by Schwerdtfeger.[46] Series of gradations of four of the major pests are analysed and the gradation divided into different stages. The following values (Table III, p. 104) are averages from a series of gradations and show the coefficient of increase in relation to the preceding year.

All these gradations are counted in the winter from the number of hibernating pupae. Large as this increase is, the real fluctuation is still larger. In the interval fluctuations do not cease, but the absolute population values grow extremely small. The 'normal' fluctuation in the interval ranges from 'nearly zero to 5–10 pupae per 100 sq. m.' This means that again in the gradation interval fluctuations are not less than 1: 100 to 1: 1,000 and that the increase-factor during the gradation has to be multiplied again by 100 or 1,000 in order to obtain the full amplitude of these pests.

Fluctuations in mammal and bird populations are smaller, but by no means as small as is often supposed. The population cycles of rabbits, lemmings, &c., in subarctic regions are certainly not much below 1 : 1,000, if not higher, and even in larger mammals fluctuations of 1 : 20–50 are common. Fluctuations are not absent in subtropical and tropical climates. The effect of the rinderpest on African wild mammals is well known. In Palestine an average fluctuation of 1 : 250 has been observed within the last few years in vole populations, &c.

TABLE III. *Gradation of forest insects in Germany. (After Schwerdtfeger)*[46]

| *Species* | *No of gradations* | *Accrescence* | | | *Progression* | | | | | *Regression* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *1* | *2* | *3* | *1* | *2* | *3* | *4* | *5* | *1* | *2* | *3* |
| *Bupalus pinarius* . . | 15 | 4·9 | 3·9 | . | 13·9 | 5·4 | 4·3 | 4·9 | 4·8 | 0·4 | 0·3 | 0·03 |
| *Panolis flammea* . . | 17 | 6·8 | 6·1 | 3·7 | 15·4 | 12·1 | 1·1 | | . | 0·185 | 0·031 | . |
| *Dendrolimus pini* . . | 12 | 5·5 | 2·1 | . | 5·0 | 7·0 | 3·8 | 4·0 | 2·2 | 0·35 | 0·15 | 0·23 |
| *Sphinx pinastri* . | 6 | 4·4 | 1·7 | 2·0 | 2·7 | 2·1 | 1·9 | | | 0·5 | 0·4 | 0·35 |

| *Species* | *No of gradations* | *Decrescence* | | *Duration of gradation* | *Product of years of* | |
|---|---|---|---|---|---|---|
| | | *1* | *2* | | *Increase* | *Decrease* |
| *Bupalus pinarius* . | 15 | 0·2 | | 11 | 137,478 | 0·00072 |
| *Panolis flammea* . . | 17 | 0·52 | 0·5 | 10 | 31,470 | 0·0015 |
| *Dendrolimus pini* . | 12 | 0·63 | | 12 | 13,518 | 0·029 |
| *Sphinx pinastri* . | 6 | 0·5 | 0·45 | 11 | 121 | 0·0016 |

Discussing these figures with a well-known physicist, the author asked him as to whether in his opinion fluctuations of this amplitude could be considered as oscillations around an average stable value. His answer was that in physics no wave exceeding the range of 1 : 10 would be regarded as such. Taking into consideration the complexity of biological processes he could still understand fluctuations within a range up to the limit of 1 : 100 being interpreted in this way. But considering the much larger range manifested in the natural amplitudes, such conception loses any real meaning and common sense.

There may exist many animal species which show little range of local abundance, as may be expected from the animals of the abyssal or from animals saturating their environment, such as blow-flies, &c., for which the oscillation around a state of average equilibrium is a conception to be permitted. But for almost all animals which show large fluctuations within a span of a few generations no such description is admissible.

Another argument used by Nicholson[33] is that 'for any given species of animal, the population density differs in different places (related to climatic or other environmental conditions). These observations clearly indicate that animal populations must exist in a state of balance, for they are otherwise inexplicable.'

The strength of this argument seems somewhat doubtful. We may compare the numerical fluctuation of imaginary animal populations in 3 different environments for 10 generations:

| *Generation* | | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Optimal | environment | 100 | 500 | 4,000 | 1,000 | 70 | 20 | 300 | 7,000 | 20,000 | 1,300 |
| Favourable | | 10 | 50 | 400 | 100 | 7 | 2 | 30 | 700 | 2,000 | 130 |
| Unfavourable | | 1 | 5 | 40 | 10 | 0·7 | 0·2 | 3 | 70 | 200 | 13 |

The amplitude always ranges from 1 to 1,000; the fluctuations are parallel. No student of the species concerned may have any doubt, after intelligent observation during some generations, that the population density is higher in the optimum and lower in the other zones. There is no need to accept any 'balance' in every district. If the environmental changes with regard to food, breeding-niches, &c., are parallel to the changes in average population density, there might possibly exist such a balance. But if, as is certainly very often the case, only strong deviations of climatic or similar factors during the most sensitive stages of development induce this change, the animal is simply passively weeded out by those factors without any active counteraction, physiological or behaviouristic, on the part of the animal concerned.

It seems that the fairest summary of all given facts is as follows:

1. All factors are of destructive value in direct proportion to the percentage per stage destroyed by each. The effect of each factor depends mainly (*a*) on the sensitivity of the organism towards the factor (which varies with age), (*b*) on the accessibility of the factor towards the species concerned, (*c*) on its range of variation and on its dependency or independency. All biotic factors are dependent, whereas climate

is independent. The control-complex does not only vary from species to species, but within the same species from region to region and from season to season.

2. Most parasites and predators have very little influence on the numerical fluctuations of their host or prey as long as the population density of the latter is low to medium. Only when a certain density is surpassed do they start to increase, and as soon as the regression is advanced (by their action or by that of other factors) they automatically recede to insignificance. The same is true for diseases, population pressure, and food, i.e. for *all* biotic factors.

3. Parasites and predators are never indispensable for bringing about the crisis of a gradation. The three main biotic factors—enemies, diseases, intraspecific population pressure —and even food will certainly make themselves felt when the gradation has passed the normal environmental capacity. They may co-operate and interchange in varying percentages or one factor may replace the others, depending on the given conditions. This fact remains the true nucleus of the differentiation between density-dependent and density-independent factors. Only the first ones may be relied upon to bring about, in their totality, the crisis of a mass-increase. Climatic regression may bring it about, but need not do so necessarily. The difference between this and earlier conceptions lies in the inclusion of all major biotic factors, instead of picking out arbitrarily the parasite component, which has no intrinsic preference over the other components (predators, diseases, population pressure, food). Small absolute destruction in later stages by parasites and predators (90 per cent. destruction in the egg means 90 killed eggs, 90 per cent. destruction in pupae only 9 individuals destroyed!) is therefore of the same importance as higher destruction of the same percentage in early development.

4. The higher sensitivity of parasites, which is observed as a general and basic phenomenon all over the world, is rather complex. It does not necessarily mean that the parasite is always more sensitive to climatic influences, despite the fact that this has been demonstrated in many cases. The parasite is dependent upon a long series of other factors, the more important of which are: (1) the host must surpass the lower

epidemiological threshold of density before any gradation of the parasite may occur (Fig. 18), and this high level of density in the host must coincide with favourable climatic conditions for the parasite; (2) the life-cycle of the parasite must fit into the local seasonal life-cycle of its host, in order to obtain normal conditions of reproduction. *Exeristes roborator* has been prevented from becoming established in North America, because of the disharmony of its seasonal cycle with that of its host *Pyrausta nubilalis*.[30] (3) The parasite must fight

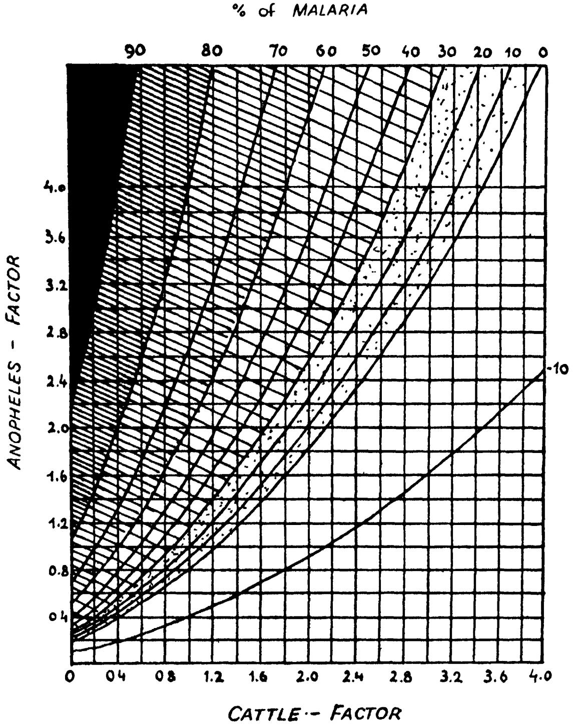


FIG. 18. Epidemiological threshold in malaria as an illustration of a lower density threshold in biotic factors. With increasing numbers of *Anopheles* the malaria dangers grow whereas an increase in the number of cattle, &c., reduces the number of mosquitoes sucking the blood of man and therefore reduces the danger of a malaria epidemic. Sudden local falls in the number of cattle are sometimes sufficient to bring about severe outbreaks of the disease. (After Martini.)

against the defence system of the prey. This fight may be through active immunization (as is the case, e.g., in *Angitia rapae* in *Pieris rapae*[31]) or through repulsion (as is the case in *Icerya purchasi* living on *Spartium* towards *Novius cardinalis*[8]). All these complex conditions are the real reason why almost no accumulation of parasitism from generation to generation is observed under normal conditions.

## 6. BIOLOGICAL CONTROL

There would have been no need at all to deal with the control of insects and other animals and plants by biological means, which have been discussed very ably by Thompson[47] and Sweetman,[48] were it not for the reason that even here misunderstandings appear in recent discussions.

H. S. Smith[32] draws the following conclusion from the author's statements with regard to the predominance of climatic control: 'It therefore follows that the introduction of parasites, predators, or diseases from the native habitat of a pest into an area where it has been introduced without them is an unsound procedure.' This wholly unjustified conclusion has been drawn neither by the author nor by any other adherent of the school of climatic control. L. O. Howard's slogan that *all* forces must be mobilized for the control of an agricultural, technical, or medical pest is regarded as a basic principle in to-day's entomology. The fact that the author has published two comprehensive papers on the successful biological control of *Icerya* and *Pseudococcus* in Palestine should have prevented such conclusions.

The theory really promoted and still maintained is that in climates with distinct seasons the mere introduction and acclimatization of an enemy will be insufficient to obtain the degree of economic control needed, as, for the reasons given above, no progressive accumulation of the parasitism from generation to generation can be expected. Every generation, or every few generations, the parasite must start from the beginning, i.e. from a very low density as compared to that of its host. In order to aid the parasite or the predator it will, as a rule, be indispensable to breed large quantities of the enemy artificially and to distribute them in density centres of the host, year after year. There is nothing new in this conception, as this is the practice which has been in use in California for many years with regard to *Cryptolaemus montrouzieri.* The large-scale 'fabrication' of the parasite plays an important role in the literature on biological control. Even in the most efficient cases as in that of *Novius* versus *Icerya* we found it necessary to breed the predator and distribute it to new micro-centres in the citrus-groves of Palestine.[8]

The only regions where permanent success has been obtained in biological control, after initial introduction and establishment, are tropical oceanic islands, such as Hawaii and Fiji, where climatic conditions are fairly constant and other environmental conditions favourable. Under such conditions accumulative parasitism may be expected. However, even there the effect has often been exaggerated. Two cases, seen by the author personally, may be quoted.

The parasitic Scoliid *Scolia manilae* was introduced against the Oriental beetle *Anomala orientalis*, the grub of which was rather destructive to sugar-cane in Hawaii. Economic damage ceased in the old centres of infestation. The large number of *Scolias* flying on every suitable spot throughout the fields of sugar-cane indicates that *Anomala* grubs must still be present in large numbers. Every digging in the soil confirms this. New damage occurs year after year in a narrow zone, mainly in the direction of prevailing winds, which is newly infested with *Anomala*. This damage disappears 1–2 years later, as soon as the *Scolia* has established itself in this zone. The *Scolia* is, therefore, to be desired from an economic point of view, since it has depressed the population density of its host below the level of serious damage. The fact that it still persists in considerable numbers is, however, overlooked.

Reading some reports from Hawaii one might come to the conclusion that the weed *Lantana* has been more or less reduced to insignificance following the introduction of a series of insect pests of that shrub. *Lantana* is, at present, one of the most common plants of Hawaii, covering—especially on lava in the wetter portions of the islands—enormous tracts in compact growth, whereas in the drier parts insects have helped artificial clearing by cultivation to some degree. What really occurred is that extensive cattle-ranging, to which *Lantana* represented a primary danger, has since been more or less abandoned on the islands.

The main reason why no fair judgement as to the value of biological control may yet be given, in most cases, is the fact that no figures at all are available. If a pest decreases following the introduction of a parasite, the importance of the enemy is established. The lack of almost any statistical observations on the mutual fluctuations of both species for a sufficiently extended period makes it impossible to draw any definite conclusions. The school of biological control should be reproached mainly by this point. And until really competent statistics of this type are available in sufficient number, no final judgement as to the results of enemy-introduction may be given, simply because no scientific analysis is possible. Laboratory experiments and extended breedings of both the prey and the enemy will have to accompany such statistical observations. There is little doubt that Tothill and his co-workers,[49] for example, have done a splendid service to Fiji in introducing the parasites of the coco-nut moth *Levuana viridescens*. But there is little doubt that wind and rain (p. 149) and other, probably climatic, factors inducing 'abnormal' mortality amongst young larvae (p. 174) are of decisive influence on the host fluctuation too. Would it not be worth while to study such problems from a dynamic and analytical point of view, instead of from one that is partial and empirical only?

May it be suggested that it seems undesirable to extend the conception of the term 'biological control' beyond the use of enemies by human agency against pests (cf.[32]). Biological equilibrium, biological balance, biotic or natural control would then be reserved for the problem of control of biotic factors under natural conditions.

The economic value of biological control has been firmly established in many cases and is beyond discussion. Unfortunately, the material at hand is insufficient to be treated by the methods of modern population analysis. Such an analysis seems indispensable for the better understanding of real natural phenomena if the theoretical background of biological control is to be thoroughly understood.

## 7. CONCLUSIONS

The problem of biological equilibrium in nature has been approached within the last decades in three different ways or by three schools of thought, which are best characterized as the biological and the climatic schools and the school of mathematical analysis. Each school has obtained results often entirely new and often apparently contradictory to those of its competitors. We should, however, state that all these schools were right in their essential results as soon as a sympathetic synthesis was attempted. We may sum up as follows:

1. The climatic school was right in pointing out that under normal conditions climate really controls population density in being responsible for the highest degree of destruction. It is, as a rule, the main factor as long as the saturation point of environmental capacity has not yet been approached. This is the normal condition for most animals and even for the longer span of life of species which are inclined to outbreaks. We were wrong to underestimate, in the infancy of our discoveries, the actual part played by biotic factors, especially during the breaking down of gradations.

2. The biological school was right in making a distinction between density-dependent and density-independent factors. Only the former may be relied upon to bring about the crisis, provided a species in gradation, or in any other way, has approached or surpassed the local specific environmental capacity. Climate may do so, but cannot be relied upon. The school was wrong in limiting biotic factors to the parasite component solely. Parasites are only one of the biotic factors: predators, diseases, effects of population pressure, and lack of food are others. These biotic factors, acting as a whole, will end any outbreak, whereas the single factors are interchangeable. The special stress laid on parasites was unjustified.

3. The mathematical analysis was in the right direction. Under suitable experimental conditions its results were verified to a very high degree. The discovery of the relaxation type of fluctuations brings the mathematical analysis nearer to natural conditions. This school was wrong in trying to

apply its conclusions, which for the time being are based on much simplified assumptions not met with, as a rule, in nature, prematurely to animal fluctuations in their normal habitat. The experimental results confirm our conclusion that all biotic factors are in principle equally important and interchangeable.

In this way the principles involved in the problem are becoming clear, with the help of all schools of thought, by combination of the essentials of all their, at first sight, contradictory results. The historical analysis shows (*a*) that most controversies were caused by ambiguous definitions, and (*b*) that the intensity and dogmatism of those controversies was in reverse proportion to the actual amount of knowledge accumulated.

# V

# IS THE ANIMAL COMMUNITY A DYNAMIC OR A STATICAL CONCEPTION?

## I. DESCRIPTION OF ANIMAL COMMUNITIES: A. MARINE BOTTOM COMMUNITIES

ALL studies of animal communities must begin with quantitative counts of the animals present in small areas. The analysis of a sufficiently large series of such counts made in a certain region allows a comparison to be made between the species and their numerical abundance in each area and permits the description of the statics of animal communities at the time of the survey.

The study of the environmental factors acting in each area as well as the study of the physical ecology of any species enables us to understand the dynamics of animal communities.

Unfortunately, the number of suitable surveys is rather small. Most of them have been done on the animal communities of the sea bottom. The surveys of Petersen,[1-3] Stephen,[4-5] Forbes,[6] Molander,[7] Shelford,[8] &c., are outstanding examples of this type of research.

It is, perhaps, most advisable to compile the results of some of these researches in order to obtain a basis for better discussion. Petersen [1-3] studied the fauna of the sea bottom in relation to production of fish food in the benthal of the Danish Seas. Quantitative catches with the bottom sampler forced upon him the conception that animal communities are the only means of dividing the bottom fauna into areas and of being able to bonitate (evaluate) the productive value of each area. Beginning with middle-sized communities (= associations of Shelford), he succeeded in distinguishing between eight such communities (Fig. 19). Table I gives a fair illustration of his results, which are the average of many catches made throughout the area of each community as well as at various seasons and in different years. His figures illustrating these eight different benthal communities are classical fundamentals of ecological teaching.

## TABLE I. *The classical communities of marine bottom animals in the Danish Seas as defined by Petersen (area unit 0·25 sq. m. of bottom surface)*

1. *Macoma community.* On all S. Danish coasts and in the Baltic. 0·3 m. depth at high water, dry at low water.

| | | No. | *Weight* |
|---|---|---|---|
| Lamell.: | *Mya arenaria* | 1 | 26·6 g. |
| | ,, *juv.* | 2 | 0·1 |
| | *Macoma baltica* | 5 | 2·2 |
| | *Cardium edule* | 1 | 11·6 |
| | ,, *juv.* | 3 | 0·1 |
| Polych.: | *Arenicola marina* | 4 | 7·3 |
| | *Aricia armiger* | 1 | 0·1 |
| | *Nephthys* sp | 2 | 0·3 |
| | Total (6) | 19 | 48·3 |

2. *Abra community (Echinocardium).* In the Baltic Sea and the fiords. 16–18 m. depth.

| | | *No* | *Weight* |
|---|---|---|---|
| Lamell.. | *Abra alba* | 10 | 1·8 g. |
| | *Macoma calcarea* | 8 | 2·1 |
| | *Corbula gibba* | 1 | 0·1 |
| | *Astarte banksii* | 20 | 12·7 |
| | *A borealis* | 4 | .. |
| | *A. elliptica* | 1 | 0·2 |
| | *Cardium fasciatum* | 1 | 0·1 |
| | *Leda pernula* | 2 | 0·4 |
| | *Nucula tenuis* | 2 | 0·1 |
| Polych : | *Nephthys* sp. | 3 | 2·7 |
| Ophiur · | *Ophioglypha albida* | 4 | 0·7 |
| Spatang . | *Echinocardium cordatum* | 1 | 3·6 |
| Crust.· | *Diastylis* sp. | 1 | 0·1 |
| | Total (13) | 58 | 24·6 |

3. *Shallow Venus community (Echinocardium).* On the open sandy coasts of Kattegat and N. Sea. 10–11 m. depth.

| | | *No* | *Weight* |
|---|---|---|---|
| Lamell.. | *Venus gallina* | 18 | 4·4 g. |
| | *Tellina fabula* | 10 | 0·4 |
| | *Montacula ferruginosa* | 4 | 0·1 |
| | *Solen pellucidus* | 1 | 0·1 |
| | *Cyprina islandica* | 1 | 14·4 |
| Gastrop.: | *Philine aperta* | 1 | 0·1 |
| Polych . | *Travisia forbesi* | 1 | 0·6 |
| | *Nephthys* sp. | 3 | 0·4 |
| | *Aricia armiger* | 1 | 0·1 |
| Spatang.: | *Echinocardium cordatum* | 3 | 43·8 |
| | *Echinocardium cordatum juv* | 18 | 34·4 |
| Ophiur : | *Ophioglypha albida* | 1 | 0·1 |
| | *O. affinis* | 1 | |
| Crust : | *Gammaridae* | 7 | 0·1 |
| Actin.: | *Actiniidae* | 1 | 0·1 |
| | Total (14) | 71 | 99·1 |

4. *Echinocardium-Filiformis community.* At intermediate depths in the Kattegat 20–22 m. depth.

| | | *No* | *Weight* |
|---|---|---|---|
| Lamell.. | *Abra nitida* | 4 | 0·1 g. |
| | *Corbula gibba* | 1 | 0·1 |
| | *Cyprina islandica* (> 3 cm) | 2 | 62·5 |
| | *Cyprina islandica juv* (< 3 cm) | 1 | 0·1 |
| | *Axinus flexuosus* | 1 | 0·1 |
| | *Nucula tenuis* | 1 | 0·1 |
| Gastrop | *Aporrhais pes pelecani* | 1 | 2·6 |
| | *Turritella terebra* | 10 | 4·6 |
| | *Chaetoderma nitidulum* | 1 | 0·1 |
| Vermes: | *Glycera* sp | 1 | 0·1 |
| | *Nephthys* sp. | 6 | 2·6 |
| | *Brada* sp. | 5 | 0·1 |
| | *Terebellides stromi* | 3 | 0·4 |
| | *Nemertini* | frag. | 0·1 |
| Ophiur : | *Amphiura filiformis* | 60 | 7·8 |
| | *Ophioglypha albida juv* | 2 | 0·1 |
| | *O texturata* | 1 | 0·8 |
| Spatang.. | *Echinocardium cordatum* | 5 | 45·0 |
| Crust : | *Gammaridae* | 2 | 0·1 |
| Pennat · | *Virgularia mirabilis* | 2 | 0·5 |
| | Total (19) | 104 | 127·9 |

## TABLE I (*cont.*)

5. *Brissopsis-chiajei community.* In the deepest parts of the Kattegat. 60–75 m. depth.

| | | *No* | *Weight* |
|---|---|---|---|
| Lamell : | *Abra nitida* | 2 | 0 2 g. |
| | *Axinus flexuosus* | 1 | 0 2 |
| | *Leda pernula* | 1 | 1 0 |
| | *Nucula sulcata* | 2 | 1 0 |
| Vermes: | *Nephthys* sp. | 1 | 1 5 |
| | *Maldanidae* | . | 2 0 |
| | *Balanoglossus kuppferi* | 1 | 2 0 |
| Ophiur.: | *Amphiura chiajei* | 12 | 4 7 |
| | *Ophioglypha albida* | 2 | 0 7 |
| Spatang | *Brissopsis lyrifera* | 5 | 90 0 |
| Crust.: | *Calocaris mandreae* | 2 | 1 7 |
| | Total (11) | 29 | 105 0 |

6. *Brissopsis-sarsii community.* In deeper parts of the Skagerrak. 186 m. depth.

| | | *No* | *Weight* |
|---|---|---|---|
| Lamell : | *Abra nitida* | 179 | 17 5 g. |
| | *Cardium minimum* | 11 | 0 2 |
| | *Axinus flexuosus* | 20 | 0 8 |
| | *Portlandia lucida* | 1 | 0 1 |
| | *Leda pernula* | 17 | 4 1 |
| | *L minuta* | 1 | 0 1 |
| | *Nucula tenuis* | 14 | 0 6 |
| Polych.: | *Aricia norvegica* | 9 | 6 0 |
| | *Artacama proboscidea* | 8 | 0 9 |
| | *Melinna cristata* | 8 | 1 2 |
| | *Pectinaria auricoma* | 1 | 0 1 |
| | *Eumenia crassa* | 1 | 1 3 |
| | *Myriochele heeri* | ∞ | 3 3 |
| Ophiur. | *Amphiura elegans* | 2 | 0 1 |
| | *Ophioglypha sarsii* | 5 | 0 4 |
| Spatang : | *Brissopsis lyrifera* | 9 | 36 9 |
| Crust | *Crustacea* | 1 | 0 1 |
| | Total (17) | >287 | 73 7 |

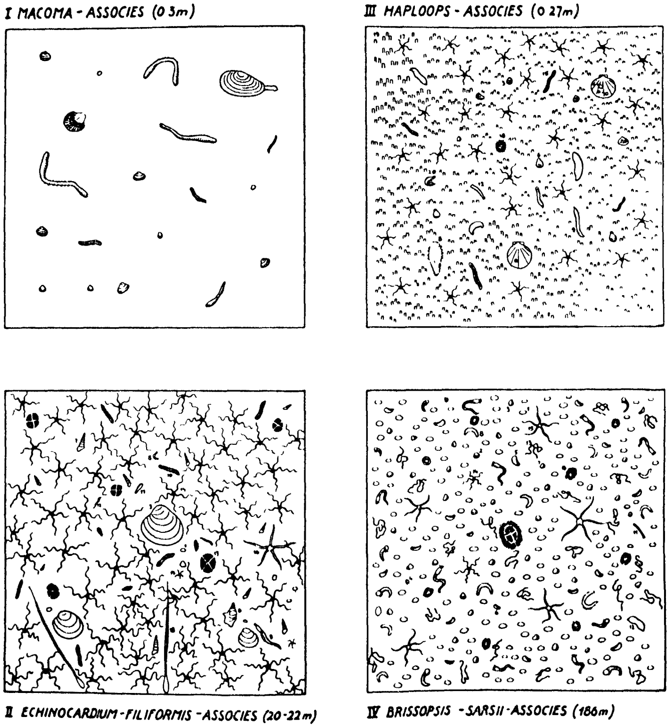
7. *Amphilepsis-Pecten community.* In the deepest waters of the Skagerrak. 320–8 m. depth.

| | | *No* | *Weight* |
|---|---|---|---|
| Lamell.: | *Abra longicallis* | 1 | 0 3 g. |
| | *Neaera obesa* | 1 | 0 1 |
| | *Axinus flexuosus* | 16 | 0 8 |
| | *Portlandia lucida* | 1 | 0 1 |
| | *Pecten vitreus* | 8 | 0 6 |
| Scaphop.: | *Siphonentalis tetragona* | 1 | 0 1 |
| Polych : | *Aricia norvegica* | 3 | 1 7 |
| | *Nephthys* sp. | 3 | 0 3 |
| | *Terebellides stromi* | 1 | 0 1 |
| Ophiur.: | *Amphilepis norvegica* | 17 | 0 9 |
| | Total (10) | 52 | 5 0 |

8. *Haploops community.* Locally in the SE. Kattegat. 27 m. depth.

| | | *No.* | *Weight* |
|---|---|---|---|
| Lamell.. | *Venus ovata* | 1 | 0 5 g. |
| | *Cardium fasciatum* | 2 | 0 5 |
| | *Axinus flexuosus* | 2 | 0 2 |
| | *Leda pernula* | 1 | 0 3 |
| | *L minuta* | 1 | 0 1 |
| | *Lima loscombii* | 3 | 0 8 |
| | *Pecten septemradiatus* | 2 | 17 9 |
| Vermes | *Aphrodite aculeata* | 1 | 10 7 |
| | *Clycera* sp | 1 | 0 4 |
| | *Eumenia crassa* | 3 | 5 9 |
| | *Maldanidae* | frag | 0 7 |
| | *Pectinaria auricoma* | 1 | 0 4 |
| | *Terebellidae* | 1 | 0 2 |
| | *Balanoglossus kuppferi* | 1 | 0 2 |
| | *Nemertini* | 3 | 0 6 |
| Ophiur.: | *Ophioglypha albida* | 1 | 0 2 |
| | *O. robusta* | 30 | 1 7 |
| Echin . | *Strongylocentrotus drobakiensis* | 1 | 2 9 |
| Crust.. | *Haploops tubicola* | 875 | 7 5 |
| | *Moera loveni* | 1 | 0 2 |
| | *Verruca stromii* | 1 | 0 1 |
| | Total (21) | 932 | 52 0 |

Molander's[7] work in the Gullmar Fiord is based on smaller communities (= faciations of Shelford) than those chosen by Petersen. The five communities of Petersen represented in this fiord are thus divided into at least 13 (faciations).



I MACOMA - ASSOCIES (0 3m)

III HAPLOOPS - ASSOCIES (0 27m)

II ECHINOCARDIUM - FILIFORMIS - ASSOCIES (20-22m)

IV BRISSOPSIS - SARSII - ASSOCIES (186m)

FIG. 19. Animal communities of the Danish sea bottom. (After Petersen.) The figures in brackets refer to depth.

Molander defines an animal community as 'a regularly recurring combination of certain animal types, as a rule strongly represented numerically'.

Stephen,[4,5] in summarizing the large Scottish survey of the bottom fauna of the North Sea, returns to the conception of animal zones, first used in oceanic research by Forbes.[6] A zone is defined as that area of sea-floor of varying width to which certain (characteristic or dominant) species are limited in their distribution. These characteristic species may either show more or less a continuity (e.g. *Tellina tenuis*) or a discontinuity (e.g. *Donax vittatus*) in their distribution. The relative density of the component species within the zone may, however, vary from time to time. The respective areas of distribution of these dominant species may also vary in position and extent.

The conception which Stephen[5] presents from the bottom fauna of the North Sea is based mainly on dominant molluscs, echinoderms being of secondary importance in one zone. The zonation is defined only for the areas with sandy and muddy bottom. The areas with a rocky bottom do not only have a different fauna, but apparently also a different major zonation.

TABLE II. *Major animal zones of the North Sea (After Stephen)*

I. *Littoral Zone.* From high-water level to 4 m. depth.
  (*a*) On muddy ground with *Macoma baltica*, *Cardium edule*, and *Paludestrina stagnalis* as the dominant species.
  (*b*) On sandy ground with *Tellina tenuis* as the characteristic species.

II. *Coastal Zone.* From 4 to 40 m. depth in the northern North Sea and 60 m. in the southern North Sea.
  (*a*) On muddy ground with *Abra alba* and *A. nitida* as the dominant species.
  (*b*) On sandy ground with *Tellina fabula* and *Nucula nitida*, or *T. fabula* alone, as the dominant species in Scottish waters. In the southern North Sea, in addition to the above 2 species *Mactra stultorum* and *Spisula subtruncata* seem also dominants. The Ophiurids *Ophiura texturata* and *O. albida* are confined to this zone.

III. *Off-shore Zone.* Occurs over most of the northern North Sea outside the coastal zone. The average density of Lamellibranches is low, no species being numerically dominant, but *Dentalium entalis* is widely distributed and may be taken as one of the most characteristic species.

The Echinoderms occur here in greatest numbers, *Ophiura affinis*, *Amphiura chiajei*, *A. filiformis*, and *Echinocardium flavescens* being the commonest and most widely distributed species.

IV. *Axinus*(= ?)+*Foraminifera Zone.* In the deep north-eastern portion of the northern North Sea and possibly extending along the edge of the Norwegian Deep. Characterized by the presence of *Axinus* (=*Thyasira*) *flexuosa* and Foraminiferan tests. All species are dwarfed.

Glancing over some of Stephen's distribution charts of single species, we must agree with him that the zone is a better definition of conditions in the North Sea than are Molander's communities. The fauna of the coastal zone in the North Sea has a slightly different composition in its northern and in its southern parts, the transition taking place gradually. More 'off-shore' species intrude into the northern than into the southern coastal area, and important differences in the dominant species occur. Still greater difficulties arise in the off-shore zone, where a very definite change takes place on passing from north to south. 'Species are gradually eliminated one after another, but there is no sharp transition and no natural break which would justify a separation into communities.'

The littoral zone with its broken mosaic of varying textures and its many half-enclosed areas is quite favourable to the community conception. The difficulty, however, lies in the fact that each observer describes 'new communities which are merely combinations in variable proportions of the same few species characteristic of one or two zones at most. Had the Scottish investigations not extended beyond the littoral zone the community concept would have been quite acceptable, but it becomes less acceptable on pushing the investigations as far as the coastal zone, and when the off-shore zone is reached it breaks down completely.'

In studying some marine biotic communities of the Pacific coast of North America Shelford and co-workers[8] obtained fundamental results. Their research, again, was limited to littoral communities which fit best into the community concept. Five communities of major rank (= biome) were differentiated with a series of subdivisions (associations and faciations). His type of classification is explained by the following list:

### Table III. *The Strongylocentrotus-Argobuccinum biome on the Pacific Shore of North America. (After Shelford)*

0–225 m. depth. Salinity and hydrogen-ion concentration fairly high. Plantation of medium abundance. Penetration of light in summer fairly great. Large algae of many species abound. Circulation of water due to tides is the most important climatic factor. Number of animals per 10 sq. m. (minimum to maximum).

*A.* Dominants

| | |
|---|---|
| *Strongylocentrotus drobachiensis* | 40–200 |
| *Argobuccinum oregonensis* | 2–50 |
| *Balanus nubilis* | 5–50 |
| *B. pugetensis* | 10–400 |
| *B. rostratus* | 10–400 |
| *Calliostoma costatum* | 2–60 |
| *Psolus chitonoides* | 1–10 |
| *Trichotropis cancellata* | 2–150 |
| *Pecten hericius* | 15–1,000 |
| *Pododesmus macroschisma* | 2–50 |
| *Amphissa columbiana* | 5–85 |
| *Crepidula nivea* | 10–50 |
| *Calyptraea fastigiata* | 3–6 |
| *Orchasterias columbiana* | 1–2 |

*C.* Influents

| | |
|---|---|
| *Icelinus borealis* | |
| *Myoxocephalus polyacanthocephalus* | |
| *Rhyamphocottus richardsoni* | |
| *Hyas lyratus* | 2–10 |
| *Cancer oregonensis* | 1–20 |
| *Oregonia gracilis* | |
| *Pandalus danae* | |

*D.* Characteristic, but rare species

*Styela stimpsoni*
*Munida quadrispina*
*Crago munita*
*Spirontocaris prionota*
*Hapalogaster mertensii*
*Pagurus kennerlyi*
*Purpura foliata*

*B.* Dominants changing with depth

*Strongylocentrotus franciscanus* 0–36 m.: few; 36–125 m.: 4–60.
*Stichopus californicus*: 5–30 m.; 35 m. : rare.
*Modiolus modiolus* 0–36 m.: absent; deep water: 10–3,000.

### I. STRONGYLOCENTROTUS-PUGETTIA ASSOCIATION

*A.* Dominants

| | |
|---|---|
| *Cucumaria miniata* | 2–20 |
| *C. chronhjelmi* | 2–30 |
| *Crepidula adunca* | 10–300 |
| *Puncturella cucullata* | 3–6 |
| *Petrolisthes eriomerus* | +++ |

*C.* Characteristic species

*Doriopsis fulva*
*Cryptochiton stelleri; Ischnochiton interstinctus*
*Polypus hongkongensis; Acmaea mitra*
*Hinnites giganteus*
*Evasterias trocchelii*

1. Nereocystis-Laminaria (Melanophyceae)—Lacuna (= Algal) faciations (0–20 m. depth).

| *Algae* | *Animals* |
|---|---|
| *Nereocystis, Laminaria, Agarum, Desmerestia, Costaria* | *Lacuna porrecta. L. divaricata, Caprella* sp., *Pentidotea resecata; Margarites succinctus; Epiactis prolifera.* |

2. Dasyopsis-Halosaccion (Rhodophyceae) (= Algal) faciation (deeper than 1).

| *Algae* | |
|---|---|
| *Dasyopsis, Halosaccion,* &c. | Animals do not show a clear-cut special community here. |

TABLE III (*cont.*)

3. Cardium-Yoldia faciation on mud bottom.

| | | | |
|---|---|---|---|
| *Yoldia scissurata* | 10–900 | *Nucula castrensis* | 2–400 |
| *Cardium californicum* | 10–80 | *Marcia subdiaphana* | 10–80 |
| *Solen sicarius* | 10–30 | *Polinices pallida* | 300–600 |
| | | *Crago alaskensis* | |
| | | *Venericardia ventricosa* | 1–100 |

4. Pisaster ochraceus faciation.

An ecotone (transition) species prevalent in a narrow zone between S.P. association and the tidal community.

*Pisaster ochraceus; Stichopus californicus; Cucumaria miniata.*

II. STRONGYLOCENTROTUS-PTERASTER TESSELATUS ASSOCIATION

Shelford's general conclusions will be discussed later on.

## 2. DESCRIPTION OF ANIMAL COMMUNITIES: B. SOME TERRESTRIAL ASSOCIATIONS

Very conclusive are the results of a study by Miss Larsen[9] on the beetles tunnelling in the sandy shores near Copenhagen. Two sections from the sea-shore towards the interior show that, at least in the Skomagerslette, clean-cut associations of these beetles exist in the different biotopes of this area.

One quantitative example, containing these beetles from 1/100 sq. m. from the sandy hills of the Skomagerslette, may be added:

| *Species of beetles* | *No. of individuals* |
|---|---|
| *Bledius rustellus* | 73·9 |
| *B. opacus* | 0·4 |
| *B. arenarius* | 0·6 |
| *Oxypoda exigua* | 3·8 |
| *Dyschirius* (*thoracicus*+*globosus*) | 5·6 |
| *Heterocerus hispidulus* | 1·0 |
| *Melanimon tibiale* | 2·9 |
| *Aegialia arenaria* | 0·6 |
| *Aphodius plagiatus* | 0·2 |
| Total no. of individuals | 89·0 |

Fig. 20 illustrates conclusively that most of the tunnelling beetles are able to choose actively their preferendum in a gradient of soil salinity or soil humidity. And this preferendum corresponds fairly well in all cases with the conditions of salinity and humidity prevailing in the normal habitat of

## TABLE IV. *Life communities of tunnelling beetles in sand*

### *A. Section through Sibiriens Havrending (near Copenhagen). (After Larsen)*

| *Niche* | *Per cent.* $H_2O$ | *Per cent.* NaCl | *Zoocoenosis* | | |
|---|---|---|---|---|---|
| | | | *Characteristic species* | *Other members* | *Predators* |
| Inundation-plain | *c.* 20 | *c.* 20 | *Bledius arenarius* | *Atheta exilis* | *Dyschirius thoracicus*<br>*D. impunctipennis* |
| Deflation-plain | Traces | Traces | No tunnelling beetles | .. | |
| Sand-plain beyond the dyke | 8–10 | 5–10 | *Bledius arenarius* | .. | *Dyschirius thoracicus*<br>*D. impunctipennis*<br>*D. politus, D. obscurus*<br>*Bembidion pallidipenne* |
| Sand-plain within the dyke | 12–14 | 20–40 | *Bledius arenarius* | *Heterocerus flexuosus* | *Dyschirius thoracicus*<br>*D. obscurus* |
| Algues-plain | 18–24 | 20–60 | *Ochthebius marinus*<br>*Heterocerus flexuosus* | *Bledius arenarius*<br>*Hypogastrura viatica* | *Bembidium varium*<br>*B. pallidipenne*<br>*Dyschirius thoracicus* |
| | | | ***B. Section through the Skomagerslette*** | | |
| Sand-plain | 10 | Traces | *Bledius arenarius* | *Melanimon tibiale* | *Dyschirius thoracicus* |
| Sand-hills | 9 | ,, | *Bledius rastallus*<br>*Oxypoda exigua* | *Bledius tricornis*<br>*Aphodius plagiatus*<br>*Hister aeneus*<br>*Bledius opacus*<br>*Aegialia arenaria* | *Dyschirius thoracicus*<br>*D. globosus* |
| Plain | 18 | ,, | *Heterocerus hispidulus* | *Oxypoda exigua*<br>*Heterocerus flexuosus*<br>*Aphodius plagiatus*<br>*Liodes ciliaris*<br>*Cercyon tristis* | *Dyschirius thoracicus*<br>*Bembidion pallidipenne* |
| Lowland covered with algae | 33 | ,, | *Heterocerus obsoletus*<br>*Ochthebius viridis* | *Helophorus nanus* | |

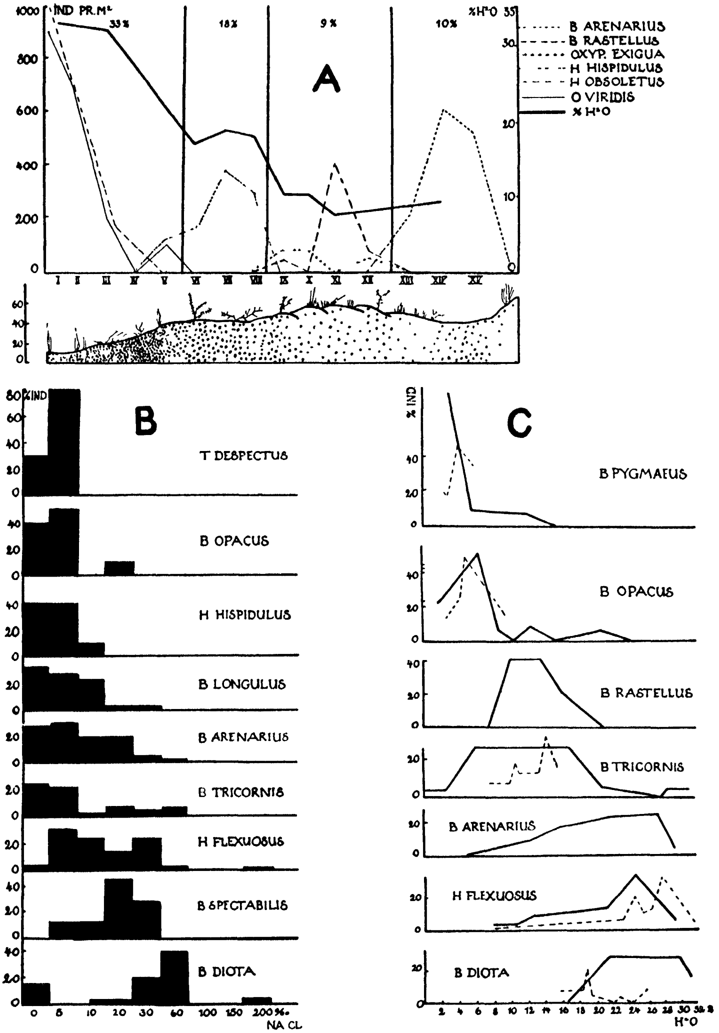


FIG. 20. Life-communities of tunnelling beetles in sand near Copenhagen.

A. Cross-section through the Skomagerslette. The curves indicate the distribution of species and of soil humidity through the different niches. The scale of the cross-section indicates the depth of soil-water surface.

B. Preference of beetles in a gradient of NaCl-content in soil.

C. Preference of beetles in a gradient of soil humidity. The broken line indicates the distribution of the beetles in their natural habitat with regard to soil humidity. (After Larsen.)

the species. It would probably be premature to conclude that these are the optima for the species concerned. It may well be that these are the optima and preferenda for the local populations of the beetles and the total range or reaction basis of the species is larger. It shows in any case, however, that the individual beetles are guided in the choice of an area by environmental conditions agreeable to them. The distribution of every species in the different biotopes shows a fluctuation of its own, independent of that of the other members of the same 'association'. Size of sand grains had no recognizable influence on the distribution of these beetles. The predators, though also dependent upon the abiotic factors of the environment, showed a high dependency upon the distribution and density of their hosts (*Dyschirius* upon *Bledius* and other Staphylinid beetles). However, as a rule, every species of *Dyschirius* shows a preference for the area of one of its hosts (*Bledius* or *Heterocerus* species; adults and larvae). On the other hand, *Dyschirius* species, generally connected with one of those hosts, may occur where no beetles of the host genera are present at all. Miss Larsen found them feeding on soil nematodes in such localities. None of the predators are definitely restricted to one host species. The fact that they show preferences for certain hosts proves that they, too, probably choose their environment following physical agreeability. It is regrettable that Miss Larsen did not include in her extensive work experiments on the preferenda of the predators for soil humidity and soil salinity.

We have been studying areas of terrestrial communities in Palestine for a number of years. Partial results for some areas and groups have been published.[10–13] But, on the whole, this survey is still incomplete and will remain so for many years to come. The areas (about 100 sq. m. on the average) have been chosen in typically developed plant-associations and have been under observation twice per month from sunrise to sunset for a whole year.

So far the results of this survey are rather discouraging from the point of view of the dynamic community concept and stress the independent distribution with regard to area, season, and abundance of every individual species. Fig. 21 illustrates this statement rather well.

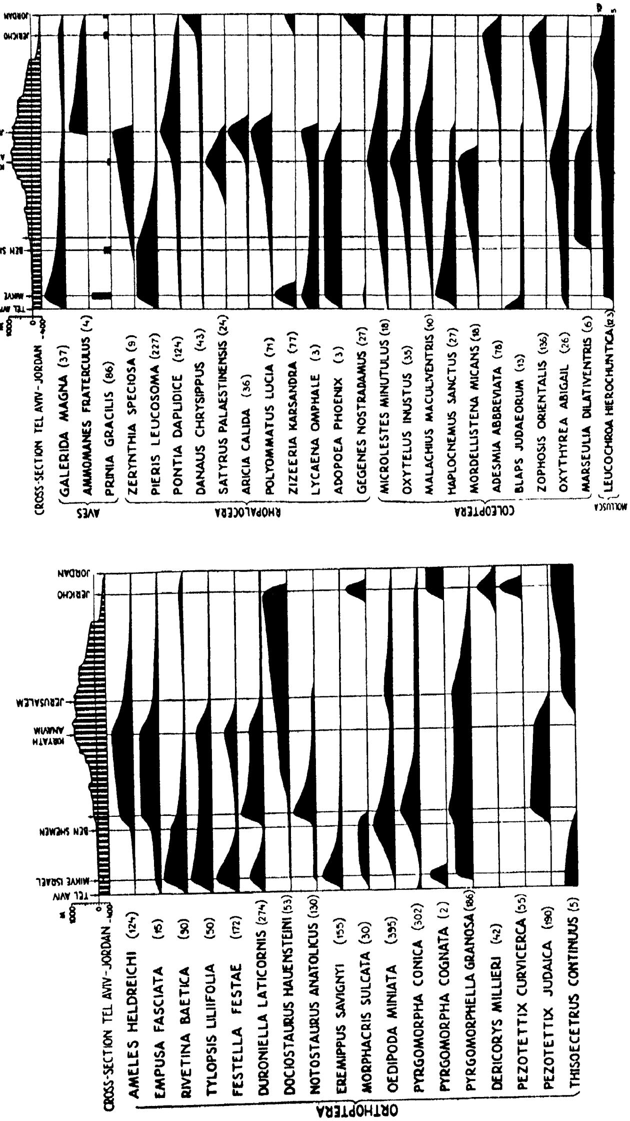


FIG. 21. Numerical abundance of various animal species in Palestine in a cross-section from the dunes near Tel Aviv to the Jordan near Jericho.

Combining the general personal experience gained during this survey with the quantitative data obtained, we arrive at the same conclusion as Stephen—that zonation is a more natural way of description than minor communities. This is decidedly true, especially for the poorer life-habitats: those of the desert and predesert, the batha (= degraded maqui), tundra, antarctic, &c. In a much variegated, 'broken' landscape of general high density of life, especially when rich in species, communities may easily be described, but every exact survey will show the same result which holds good for marine littoral communities of minor rank: the number of communities grows embarrassingly with every survey, and the difference between them is a permutation amongst a small number of always reappearing dominants, whereas the number of rare characteristic species is more and more reduced to monophages on a typical plant. This experience does not support the theory of equilibrated life-associations with highly integrated superorganistic structure and function.

It may be added that the phenomena of diurnal and seasonal succession, of stratification, and of vagility make the terrestrial animal communities a rather complicated study.[12]

Boycott[14] states that British land Mollusca do not form specific associations with one another or with other animals or plants. Competition is of no importance as a limiting factor. If we arrange the Mollusca of various habitats according to the number of Mollusca living in them, we find that the kinds which live in the poorest places live also in the richest ones. The progression consists in the addition of fresh species without the elimination of those already on the list.

'*Arion ater* is probably the most ubiquitous species and often lives by itself on acid inhospitable moors. *Agriolimax agrestis* is almost as universal and *Arion minimus* not much more particular. Among testacea *Hyalinia alliasia*, *H. fulva*, *H. radiatula*, *H. cristallina*, *Punctum pygmaeum*, *Helix rotundata*, *Colchicopa lubrica*, or *Vertigo edentula* are most likely to be found if any snails at all are discoverable. Which of these is found depends apparently on the nature of the badness and decidedly on geography. All these species are also common in the "best" places, which may show nearly 40 species in a small uniform area (e.g. old calcareous beach wood). The same is true for the

> Mollusca of specialised habitats such as marshes or chalk downs: the species which in some places occurs by itself or with few associates will also be found where the full fauna is present. I do not think that (with a few exceptions) a snail is ever excluded from a locus suitable for it because other snails are there already or that one species can "expel" another.'

Their occurrence within their geographical range is therefore determined by history and the nature of the habitat, where moisture and lime are of paramount importance. The moisture is determined by environmental structure as shelter ('nooks and crevices into which Mollusca can retire to escape drought and cold and lay their eggs'). Exposure to wind is objectionable, whereas a certain air circulation is necessary. Dampness determines the amount of time a mollusc can spend in feeding and breeding per annum.

In Britain groups of snails inhabiting wet places, dry ones, and human settlements may be distinguished. The rest, about half of the species, lives in ill-defined 'woodland' habitats the suitability of which varies in proportion to the shelter and lime they provide. With regard to lime there are: 1 calcifugous species, 20 calcicoles, 18 which prefer lime, and some 45 which are indifferent (within a certain range!).

The same author[15] comes to almost identical conclusions with regard to the fresh-water Mollusca of Britain. These are not dependent upon other animals except that *Anodonta* and *Unio* have an obligatory parasitic phase on fish. Nor have they any specific food. There are indications that the habitats of a few species are partly determined by competition with other Mollusca. Species as *Limnaea glabra*, *Planorbis spirorbis*, *Pisidium personatum*, *Physa hypnorum* are found in bad habitats only, where no other species thrive, whereas they do not occur in favourable loci.

> 'But in general competition is unimportant and most of the species which occur in the worst places are found also in the best. Hence each species can live in any place where its characteristic needs are met by the physical and chemical conditions. (Cleanliness of water, absence of disturbance and presence of lime are favourable.) With a few exceptions, the needs of the species are so similar that habitats can be classed as good or bad for Mollusca as a whole: the richest places are calcareous rivers, lakes and canals, the poorest rapid streams, mean ponds and mountain lakes.'

## 3. THE HABITAT CONCEPT OF ANIMAL COMMUNITIES

Repeated attempts have been, and will be made, to describe animal communities by the extrinsic factors of the habitat. Type of soil, type of vegetation, average temperature or humidity, salinity, &c., range of fluctuation of the latter, &c., should always be registered. But following our present experience, those descriptions are never sufficiently neat to explain the absence of other communities and their dominant members. Petersen[3] states:

> 'At first it was thought possible to determine those zones by the depth alone or by a characterisation of the vegetation and bottom conditions, but though much has been gained along these lines we do not hereby come to the kernel of the matter, namely, the occurrence of the generally distributed animals, which alone can tell us where a certain animal community belongs, even though the depth and outer conditions may vary.'

The description of animal communities is therefore a primary task.

Shelford[8] holds a more optimistic view, also based on benthic communities of the littoral. The two subtidal biomes recognized differ in speed of water circulation, salinity, penetration of light, plankton density, and quantity of detritus. Shelford generally maintains that 'the general hydrographic conditions (submarine climate) are more important than kind of bottom materials in determining the character of benthic communities'. In his opinion the communities should form part of any physical survey.

It is an uncontestable fact that terrestrial biogeographical regions and zones may be characterized very neatly by climograms based on monthly averages of temperature and precipitation of the average macroclimate of these zones. It is more surprising to find that the differences between the climograms are, at least in Palestine, about as large in the average territory occupied by every region in Palestine as are the average differences in the macroclimates of the Mediterranean (= maqui), Saharo-Sindian (= desert), and Irano-Turanian (= steppe) regions in general.[12] The importance of the macroclimatic climograms is really surprising in view of the fact that this macroclimate is purely an idealization of a large and varying range of different eco- and micro-climates. Certain types of soil and vegetation are correlated with each zone.

The selective power of an unsuitable environment has been beautifully demonstrated by Lundbeck[16] for *Chironomus bathophilus* in the Lake of Ploen. The eggs of this gnat are indiscriminately distributed over the whole surface of the lake. Projecting this surface area to the different zones of depth within the lake, out of 68 milliards of eggs, 16 milliards should drop to the bottom at 0–16 m. depth, 50 milliards at 16–36 m., and 2 milliards at 36–44 m. depth. What actually occurs is as follows:

| *Depth* | 6. vi. | 11. vii. | 31. vii. | 5. ix. |
|---|---|---|---|---|
| 0–7 m. | . . | . . | 52 | 489 |
| 8–16 m. | . . | . . | 2,133 | 1,045 |
| 17–26 m. | 199 | 968 | 5,967 | . . |
| 27–36 m. | 267 | 256 | 649 | . . |
| 37–44 m. | . . | . . | . . | . . |

This shows that all eggs sinking to the bottom of the lake beyond the zone of 16–36 m. depth die. The intrusion into higher strata is a secondary larval migration. Animal zonation is here decidedly a selective process after indiscriminate dispersal.

The story of the plaice (*Platessa platessa*) in the North and Baltic Seas is another striking example of this type.[17–21] The plaice population of the Baltic Sea is unable to maintain itself because unfavourable hydrographical conditions (salinity, temperature) reduce even its enormous egg-production to far below the level of the parent generation.

However, sufficient as the external factors may be to give a good idea as to the general character of the environment of every zone, they are certainly insufficient to 'explain' the distribution of the species. Many analyses of individual species have aimed to reach this purpose by describing the physical ecology of each species in as much detail as possible. It has not yet been possible and will probably never be so to reach this aim. Zones or conditions of optimum, favourable, unfavourable, and impossible environments have been circumscribed and hold good in rough outlines when compared with the facts. But optimal zones remain where the species is absent or has a low population level due to obscure (does this always mean: not yet analysed?) causes; there are impossible zones where a moderate population is constantly maintained, and there are zones of equal bonitation where the population level of the same species is very different. None of the combinations of factors studied in connexion with physiological tolerance have ever explained satisfactorily the local distribution and limitation of any animal species, be it in a terrestrial, soil, freshwater, or marine space. And this elusiveness in the physical ecology of an animal has its well-founded reasons.

We are now leaving the period in which animal ecology regarded the animal as an object solely. We are learning that the responses of an animal to its environment are different from those of any non-living object. The animal reacts actively by changes in behaviour or by regulations of its physiological or morphological function or structure. A few of those physiological reactions or reconstructions are quoted herewith to explain our case. The thermo-hygrogram of an insect often changes from generation to generation according to the sequence of environmental influences acting on the preceding generation, as well as on the previous development of the generation concerned (i.e. its history). Shelford[22] has demonstrated this for the chinch bug, Zwoelfer[23] for the nun-moth, and Bodenheimer[24] for the red scale. Whereas the position of the vital optimum is not shifted at all, the distance between the isothanates (= lines of equal mortality), expressing the sensitivity and tolerance of the animal to temperature and humidity, varies. The physiological resistance and vitality of the same species towards the same combination of environmental factors is therefore different in various generations and years.

Information has only recently been gathered on the shift of other physiological activities within the area of distribution of the same species. It has become a well-known fact that the thermal sum needed for the completion of one generation is often decidedly smaller on the northern border of the area of the same species, than within the centre or the southern part. Owing to this adaptation alone the animals mature in time, and in those cases where the animal is unfit to pass two winters in an immature stage negative selection is perhaps the reason for this phenomenon.

Physiological adaptation or toleration may occur in widely distributed species. Mayer[25] found in *Aurelia aurita*:

| | *Average surface temp. in summer* | *Limits of activity (pulsation)* |
|---|---|---|
| Nova Scotia . | 14° C. | −1 to 29° C. |
| Florida . . | 29° C. | 12 to 36° C. |

Fox [26–7] reports for 7 pairs of species of marine invertebrates inhabiting southern English waters and more northern seas respectively that the oxygen consumption of the warmer-water species is greater than that of the colder-water species in their normal environmental temperatures, although the locomotory activity of the former is apparently not greater. He suggests that the similar locomotory activities of both species require approximately equal amounts of oxygen, but that the non-locomotory oxygen consumption of the warm-water species is higher than that of the cold-water species. The same is correct for the cleavage of eggs of sea-urchins from England and Southern France.[26] This theory is compatible with similar studies made recently on marine algae.

The increase of respiration-intensity of salt-water organisms entering brackish or fresh water is well known. It is expressed by the distribution of certain Crustacea which can live in fresh water only in the coldest parts of lakes, where the oxygen need is still relatively low, whereas at higher temperatures it exceeds the respiration facilities. The behaviour of the amoeba *Mayorella palestinensis*,[28] which grows in zones of different depths (i.e. at different oxygen tension), in cultures of various H-ion concentrations (8·2–5·7) or of different NaCl concentrations (1·0–0·0 per cent.), is probably connected with changed behaviour towards oxygen tension. Towards acidity and towards lower salt concentrations the zone of growth falls, i.e. the amoeba grows positive to a lower oxygen tension. In concentrations of dextrose from 0 to 2 per cent. no influence on the reaction to oxygen tension is recognizable.

All these facts tend to show that in a changed environment within the area of distribution a real physiological reconstruction of the organism occurs quite regularly with regard to the local range of certain factors. The recent studies on 'Abbau' diseases of potatoes confirm this view-point. The conclusion to be drawn is that the species is really composed of very different physiological populations or lines which are grouped geographically and conditioned by a different range of certain environmental factors, which is one of the main reasons why any absolute and really conclusive physical ecology of any animal species is impossible. For this reason, a detailed habitat description of the environmental conditions necessary for any animal community is not feasible. Whereas animal communities exist and are correlated with certain macroclimatic soil and vegetation types, no definite physical limitation can be given or be expected either for the community or for the individual species which are its members.

### 4. EMPIRICAL SPECIES COMBINATION, AS CHARACTERISTIC OF THE ANIMAL COMMUNITY

The conclusion to be drawn from all the above remarks is that, as a rule, each animal species has its highest density and its limits in accord with the optimal, or, alternatively, the intolerable, features of the environment. Whereas the reaction basis of almost every species is somehow different from that of all other species, the areas of no two species are probably exactly identical. However, this difference may be smaller or larger and the areas of the species will vary in accordance with these differences. If a series of animal species is constantly met with in certain niches or biotopes or plant associations, this simply implies that they find here suitable or optimal conditions. They therefore thrive within this area each in his own right and not as a member of an animal association.

This does by no means exclude the fact that certain animals depend on the presence of other animals, as is obvious in the case of specific or oligophagous parasites, predators, and true symbionts. It is also obvious in the case of coprophagous scarabaeid beetles, which depend on the presence of large phytophagous mammals for food and reproduction and, again, in the case of animals developing in carrion, to the presence of which they are confined. Other species depend entirely on the presence of other animals whose deserted holes, &c., they use as a regular habitat or as breeding niches. But in all these cases the inter-related or coacting animal belongs to the environmental conditions required for existence. And in any one of these latter cases the relation is quite one-sided: the mammal may live in the absence of any scarabaeid beetle, &c. The mixed herds of antelopes, gazelles, zebras, giraffes, ostriches, &c., may likewise not be called associations, as the presence of one species is not essential for the existence of the others. However, living in the same habitat which suits their environmental requirements, they may or may not mix, according to their social temperament.

The vegetation is likewise important: in the case of mono- or oligophagous vegetarians it constitutes the food or the host for development. However, it is more important as a part of the physical environment, creating microclimatic, and other conditions, or breeding niches, favourable or unfavourable to certain animals.

This conception does not exclude the presence of competition. Darwin was the first to realize that competition is strongest amongst the members of the same species. This is logical, as the niche of these individuals is more or less identical, in any case more identical and overlapping than that of the individuals of any other species. Whereas intraspecific competition is strongest, it decreases interspecifically with the increase in the difference of the reaction basis. Animals of the same group are therefore the most important competitors and often the only real competitors (ants against ants in Hawaii, earthworms against earthworms in South America, white man against red man in North America, &c., as against competition of cattle and rodents in grazing). Nor is this conception incompatible with the theory that the presence of one animal species may prevent the intrusion of another one.

It therefore seems that the animal association, its creation as well as its structure, is a chance one which is created by history and selection. The selection is negative, as it excludes species which find the habitat unsuitable and is also active, for animals are positively attracted by their senses to their preferred habitats in many cases. This becomes especially conspicuous in dysharmonic (extreme) habitats, where the inhabitants show a surprisingly high agreement in their taxisms, which is not the case in harmonic habitats.

There is no doubt that there exist animal communities of different orders, characterized by the abundance of some species, the dominants, and by the presence of mostly only a few individuals of other species more or less restricted to one community only, the characteristic species. But each member is a more or less independent member of the community, existing in it by right of its own ecological tolerance towards the specific environment (including climate, food, &c.). The composition of the community is constant with regard to its dominant and characteristic species because of the common physiological and ecological behaviour of these species. The relative as well as the absolute abundance of each member species of the community fluctuates from season to season, from year to year, and in longer periods, parallel to fluctuation of environmental factors.

The dominant and characteristic species of any community belong to the community, for they display similarly favourable response to the main environmental factors present in the area covered by the community. The latter is therefore a purely statistical or empirical conception, which is useful in ecology as well as in zoogeography. As the community depends on the same factors which form the environment, it also plays an important role in any description of that environment (local environment as well as type of environment). Shelford[8] proposes therefore, for example, to include the community survey in any hydrographical marine survey.

Whereas the classification of the different ranks of communities is largely left to the personal discretion of every student, in principle the nomenclature and classification proposed and applied successfully by Shelford is to be recommended as a sound basis for further work.[29]

Should any type of dynamic association be recognized, the conception of the bio-community is certainly preferable to the independent treatment of animal and plant community, where vegetation or animals only appear as parts of environments. Even if associations are recognized only in the statistical and descriptive sense, descriptions of bio-communities are preferable.

For all the above-stated reasons it seems inadvisable to retain the terms autecology and synecology in their original meaning. But with some slight change they fit well into an ecology without dynamic animal associations. Autecology remains the study of the reaction basis of any animal species and attempts to get at the fitting in of this reaction basis into the natural environment, or the sequence of natural environments in which the animal lives. Synecology does not remain the study of the integration in associations merely, but becomes the study of prevalent animals in different biotopes on the one hand, and of all possible association of any individual species with other animals and plants in nature on the other hand.

### 5. DO COACTIONS WITHIN THE ANIMAL COMMUNITY JUSTIFY THE SUPERORGANISTIC CONCEPTION?

It would be premature to conclude that within animal communities, zoocoenoses or better biocoenoses, every species reacts as if it were alone and isolated. We know definitely that individuals of the same species, as soon as they surpass a certain intraspecific density, decidedly disturb one another, which is expressed—if not alleviated by mortality or emigration—in lower fertility, under-nourishment, shortened longevity, &c. The sum of individuals of any one species within one area shows the reactions of a superorganism upon the setting in of intraspecific population pressure. The mutual pressure (= interpressure) of any two species inhabiting the same community is greater when the two are more similar in their ecological demands and niches, and smaller when their ecological needs overlap slightly or not at all. In these cases it is not a question of mutual help but of mutual toleration, of empirical equilibrium maintained between those species. The numerical equation depends entirely on the environmental conditions and the reaction basis of these species.

The coactions of animals are mainly on the food basis. The weight of all predators must always be much lower than that of all food animals, and the total weight of the latter much lower than the plant production.[30] Ratios of 1 : 10–30 have been found amongst those groups, i.e. 1 predator : 20 food animals : 400 vegetable matter. But although reproduction goes on at a more rapid rate in the prey than in the predator, as a rule, owing to the smaller size of the former, it is devoid of any meaning, and a real dynamic evaluation of numeric relations of the different layers of the food pyramid of any animal community has not yet been obtained. But it does not seem just to conclude from the mere maintenance of the food pyramid within any biocoenosis that intrinsic regulations occur within the community. For any individual species we have as many examples of coincidence of fluctuation of prey and predator as of those which show a complete independence (see Fig. 22).[31,32] Whereas a predator is able to maintain itself permanently only in those communities where the fluctuation of the total normal food never falls below the level necessary for its maintenance—even during the poor season—it is obvious that the importance of absolute food quantity present is of primary regulatory importance. Wherever the predator preys too much, he destroys the life community on which his existence is based. The permanent maintenance of large territories per family is therefore a common feature among small and large predators. After this behaviouristic exclusion of food competition its regulatory function is excluded to a certain degree. The question may be raised—it cannot yet be answered by the scanty material at our disposal—as to whether the absolute limitation of food is at all a common and important limitation in normal environments. Almost all facts available point to the negative. It becomes more and more obvious that limitations are primary within the animal itself. A most illustrating lesson in this respect is the sequence of Planarians in springs in central Europe. Experiments show:[33]

| *Species* | *Temperature in nature* | *Optimal temperature* | *Instantaneous death* | *Habitat* |
|---|---|---|---|---|
| *Planaria alpina* | 0–10° C. | 3–7° C. | 30° C. | The origin and coldest part of the spring. |
| *P. gonocephala* | 12–20° C. | 15° C. | 32° C. | The later and warmer part of the spring. |

Temperature has a determining effect as far as it determines the general tonus of activity. *Planaria alpina* does not differ by much in its absolute temperature tolerance from *P. gonocephala*, but above 10° C. it grows lazy, whereas its

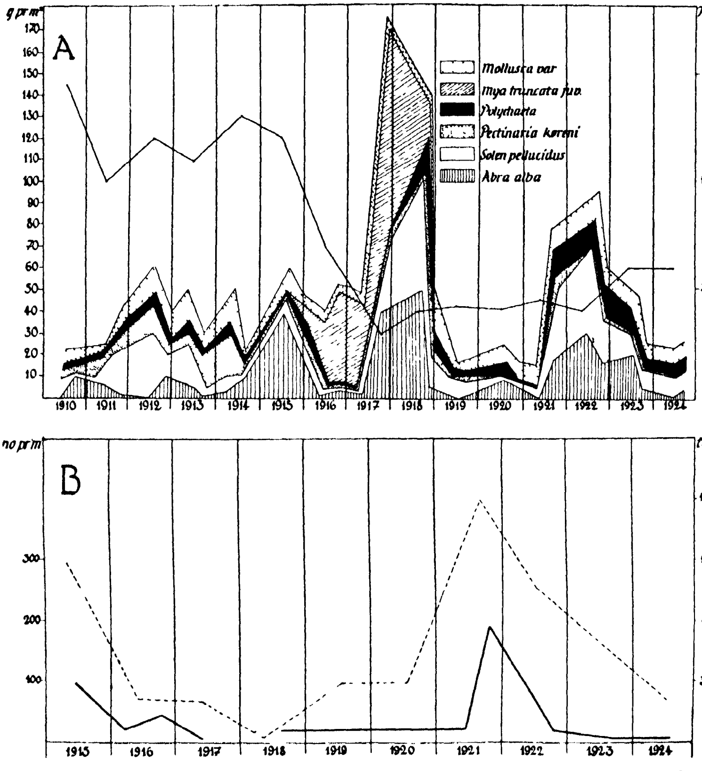


FIG. 22. Fish food and fishery yield in Danish seas. A. Quantity of fish food (gm. per sq. m.) and yield of plaice fishery (in tons: broken line) in the Thistal broad during 1910–24. B. Number of *Solen pellucidus* (per 1 sq. m.) and yield of flat-fish fisheries in the Fur Sound-Risgaard brood during 1915–24. (After Blegvad. The curves for 1915 and 1922 deviate slightly from the original.)

food exigencies are higher. It starves itself as consequence of this discrepancy in physiological behaviour and nutritional needs. The reverse is true for *P. gonocephala*, the activity of which is low at lower temperatures and below the level of metabolic maintenance as well as below that of active feeding. The mutual replacement of these Planarians is therefore not based on competition and no intrusion into the area occupied by each *Planaria* occurs, even if only one species occurs in one spring.

Coactions (interactions between organisms) occur in large numbers within any animal community. Organisms create conditions for the development of other species, even apart from the food problem. But it does not seem probable to-day that these coactions make the community a real one, a system of labile equilibrium of species interacting in the most manifold ways and integrating the members of a community into a real superorganism.

The biocoenosis has been claimed mainly by fresh-water biologists as a superorganism from another point of view, which may be called the physiological view.[34] Considering the total circulation of organic and inorganic matter within a closed system as a pond or a lake, a certain analogy to the metabolism of an organism may be discovered. But this circulation of matter in a closed, autarctic system is nothing more than an analogy. It simply means that the nutritional salts are used for the production of the autotrophic flora, which is being used in turn by smaller animals which serve as food to fish. All remnants are decomposed by bacteria, and their matter again enters the circle of production either as detritus circulated by detritus-feeders or as nutritional salts utilized by the autotrophic flora. This system is therefore not to be compared with the metabolism of an organism which requires purposely and selectively the matters necessary for the maintenance of the organism from outside, and which has a complicated physiological system of internal dissimilation, assimilation, transport, and distribution of matter. One joint of the circle interrupted, the organism breaks down. However, in the lake, life, perhaps in the form of another life-community, would be maintained if no fish were present or if bacterial decomposition were quite incomplete. The only conclusion to be drawn is that here also the relations of the food pyramid are maintained. An empty food space within an harmonic environment always calls for a filling up with suitable organisms of the neighbouring biotopes. The mere fact of the maintenance of the food pyramid cannot be regarded in this case as a proof for superorganismic structure of the life-community.

A strong additional argument against the superorganismic structure of animal communities is their mode of establishment and their longevity. The latter depends entirely on the stability of the environment. In the stable environments of the abyssal, pelagic, benthal zones of the sea conditions are fairly stable over many secular or even over geological periods, whereas the littoral community exposed to the rise or fall of the shore, the erosion of the tides, &c., is entirely unstable. Once the conditions change, the life-communities follow quickly. Shelford[8] states for the *Balanus-Littorina*-biome on rocks as well as for the *Macoma-Paphia*-biome on sandy beaches, that they develop within a few months.

> 'Succession is evidently slowest where suitable soils or other substrata must be built up with the aid of organisms, e.g. in the *Strongylocentrotus-Argobuccinum* biome where a bottom of shells must be built on mud or sand bottom. . . . All the communities studied are characterized by short life-histories (of the representative species) and rapid replacement; hence, also rapid development and quick response of community composition to minor changes in external conditions.'

These statements are entirely true for terrestrial communities too. After draining a moor, we observe the speedy replacement of the bog-biocoenosis by a transition of series of plants and animals up to the establishment of the new community. This transition lasts for 5–20 years, depending on the degree of drainage and final character of the area. But as soon as the soil has grown 'mature' and becomes stable, the new community is established within 1–3 years. This means that community changes depend on the rapidity of the environmental changes solely. If a new environment is established rapidly, the new animal community is also rapidly formed. If the transition is slow, the formation of the community is also gradual and slow. The community does not undergo a natural growth-cycle in which successions of different stages of maturation supersede each other ending in death, but its growth and death are entirely unorganismic, depending solely on the permanence and stability of the physical environment. The same is true of their longevity, which is not dependent on intrinsic (physiological) factors but on extrinsic

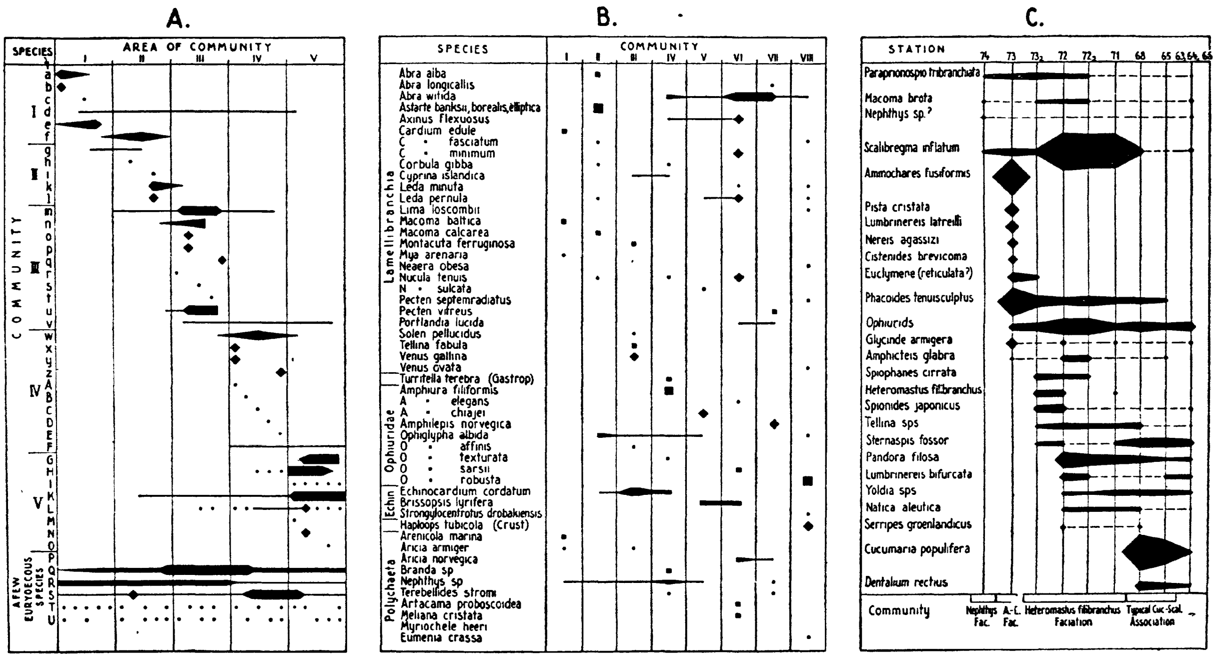


FIG. 23. Distribution of numerical abundance of dominant species in different habitats of the sea-bottom. A. Scheme of such distribution. B. Characteristic species of the eight main animal communities on the Danish shores. (After Petersen.) C. Cross-section through the faciations of the *Cucumaria-Scalibregma* association on the Pacific shore. (After Shelford.)

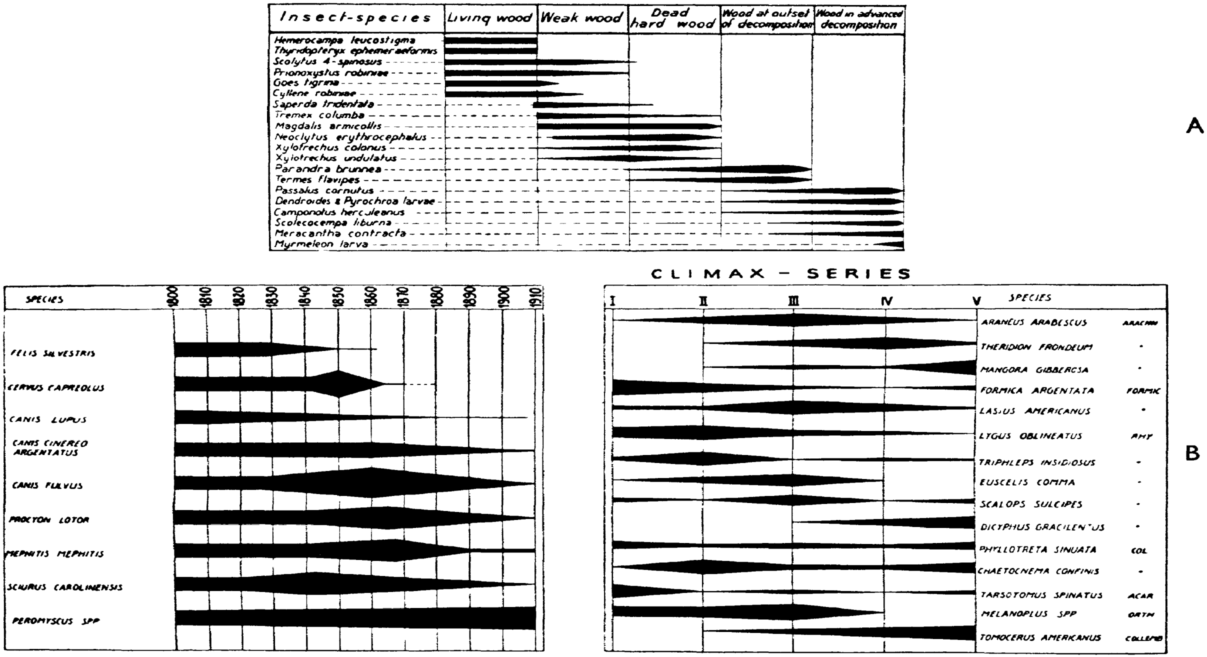


FIG. 24. The numerical change in shifting terrestrial animal associations. A. Insect succession in dying wood in Illinois. (After Shelford.) B. Shift in abundance of nine mammals in Illinois following human settlement. (After Wood.) C. Insects of the climax-series of the red oak-plane tree wood. (Greatly schematized, after Smith.)

(environmental) ones purely; i.e. longevity in the organistic sense does not occur.

The fact that plants and animals of any community may change their environment and thus create new conditions for another community of the same climax-series, i.e. the phenomenon of succession within one climax-association, is entirely independent and does not interfere with our argument, but, on the contrary, confirms it. Series of successions are conditioned by change of environmental conditions, and each member of a series enters, flourishes, and disappears from this succession on its own accord. It is the human mechanism of thought which chooses the dominants selected at certain intervals in the succession sequence as indicators of community shift.

The animal community as an empirical or statistical conception is compatible with the descriptions, deductions, and conclusions of all those workers who have made surveys of their own in the field. It is compatible with the original and most widely accepted definition of biocoenosis as a 'population system in labile equilibrium which appears at certain ecological [read: environmental] conditions' (Resnoy) as well as with the oldest definition of the biocoenosis by Moebius.

This conception is further compatible with the idea that the vegetation and the fauna of any landscape have general traits in common. In a desert where lack of water in any form is the dominant factor all life is dominated by this one factor. The same is true of animals living in the abyssal, pelagial, littoral of the sea or in the tundra or a tropical rain-forest. The 'genius loci' (Caradja) of each major habitat is expressed by common traits in sociability, breeding-stratum, colouring, body-size, &c.

However, this conception is incompatible with the conception of the animal community as a mystic holocoen (Friedrichs)[35] or as a dynamic superorganism as long as it is not founded on facts but on intuition only. The author is inclined to believe on the basis of the general development of ecology that the final solution of the problem of the real character of animal communities will be a compromise. The numerous processes of coaction within such a community are often quite primitive. In other cases they may lead to a beginning of integration into a higher form of real organization.

In the case of small monospecific communities (as are the families of social insects or human peoples) the integration may even reach a true superorganistic structure.

But it does no justice to the way of biological thinking to anticipate by deduction (philosophy) or by *a priori* intuition results which can be obtained only by means of minute biological methods. The author will gladly accept the accusation of being a non-musical person, unable to perceive the music of nature's composition, the music of the spheres. Real progress in biology is not made by 'feeling', but by understanding. Intuition may serve as a first guide to start work on unsolved problems, but it is not identical with the anticipation of scientific results.

We may define animal communities tentatively as a combination of (plants and) animals, recurring in an approximately similar composition, with regard to the dominant and characteristic species at least, wherever similar ecological conditions exist within the same zoogeographical territory. Identical habitats in different zoogeographical regions show a surprising analogy and homology in the composition of their life-communities. This similarity is the outcome of selection: negative selection by the environment, positive selection by similar taxisms and behaviour. Within the animal community occur interactions between animals and plants, but even beginnings of any real integration of the members of the biotic community, the biocoenosis, to a superorganismic structure is extremely rare. As a rule, each species exists within the community on its own right, which is expressed by the area of each species conditioned by its own reaction basis, different from that of all other species. No active co-operation occurs in the animal community, but at the utmost, a certain mutual tolerance of the species, the niches of which overlap to some degree. The animal community is therefore a useful empirical and statistical conception, facilitating the description of animal life in various habitats, but not a dynamic, superorganismic reality. Considering the lack of organismic behaviour, for example, with regard to growth, metabolism, longevity, which the biotic community shows, the application of the term sociology (as used in botany) is out of place.

# VI

# THE INTERACTION OF ENVIRONMENT AND HEREDITY WITHIN THE ORGANISM

## I. ACTUAL RELATIONS BETWEEN ECOLOGY AND GENETICS

'TO ask whether heredity or environment is the more important is like asking whether the area of a rectangle is more dependent on its base or its altitude.'[1] This clear expression of an American student characterizes the polar relations between the two branches of biology, genetics and ecology. Whereas no anterior, northern, &c., pole is imaginable without the presence of its counterpart, a posterior, southern, &c., pole, no organism is imaginable not subject to both major forces, those of heredity and those of environment. Both forces work on the organism, which in turn responds to both by action and reaction, and in this way its many potentialities are realized.

Considering this close essential connexion between constitutional and environmental factors within the organism and their permanent mutual interrelation, close co-operation ought to be expected between the students of both branches of biology. To our surprise, however, we find almost no co-operation, even no mutual discussion of basic problems. This lack of co-operation seems to be the consequence of different stages of development of both sciences, resulting in widely differing maturity and widely differing methods.

The problem of heredity has been recognized as one of the basic problems of biology since the days of Lamarck and Darwin. Variations in plant and animal were studied and statistical methods have been applied to them since the days of Johannsen. The rediscovery of the Mendelian laws introduced quantitative analysis and prognostic methods of individual hereditary characters. However, genetics really became mature only after Morgan's ingenious foundation and quantitative demonstration of gene structure within the chromosomes of *Drosophila*, and after the foundation of development-mechanics by Roux and Spemann, which approaches the genetical problems from another angle. Now it became possible to obtain clear-cut answers to clear-cut questions by *experimenta crucis*, provided the genetic structure of the parents to be crossed was known. But this type of experimentation, which always yielded quantitative results proving or disproving any theory, eventually, after a suitable change of the original plan of experimentation, resulted in a self-certainty which is rather characteristic of the genetical way of thinking of our time. The geneticist refuses any conclusion which cannot be demonstrated and proven by experiment. The experiment is certainly one of the basic methods of biological argument, and the results of genetical experimental methods in our generation certainly justify the pride of these workers; but they forget that negative experimental results bear a great deal less weight in biology than positive demonstrations. They forget that the development of almost any branch of biology shows that nature very rarely chooses *one* principle only, *one* solution only for any morphological, functional, or psychological problem.

Animal ecology is a relatively young science in comparison with its older sister. Conclusions drawn by analogy or coincidence still play a major part in our thinking. Shifts of population density coinciding with parallel trends of temperature, precipitation, &c., are regarded hypothetically not as analogous, but as causally connected. Should the inadequacy of any such connexion be demonstrated, a new theory by analogy would, as a rule, easily be formed. The growing empirical registration of facts, trends, and analysis under different conditions gradually improves the conclusions drawn and makes them more and more reliable. The introduction of physiological laboratory methods, which are still at their first beginning, opens important ways of checking the theories gained by analogy. But the ecological interpretation of facts will always be less reliable than the genetical one. In genetical experimentation the genetical structure (at least with regard to qualities concerned) is quantitatively known, if not at the beginning then at the end of the experiment. Environmental factors are generally kept uniform or are at least well known. In ecological experimentation we may study the influence of one factor or one combination of factors—other conditions equal or known—experimentally.

But in nature the interaction of all factors changes the value of the experimental result to such a degree that no conclusive deduction is possible. Moreover, whereas the ecologist experiments with constant factors or with known changes in a limited set of factors (temperature, light, &c.), the influence of the physical environment is often different in nature. Moreover, the various successive stages of an animal often have very different optimal zones and show a varying sensitivity towards external influences at different ages. The environmental factors often have a major influence during one or two very short stages of development, and if this stage (often a few days only out of a long-lasting egg-stage) is not included in the experiment, only inconclusive results are obtained. And, finally, in almost every case the genetical structure of the animal concerned is absolutely unknown. Who will reproach the geneticist for preferring his pure, clear-cut kind of thinking to this chaotic state, where methods and results are obviously still in an early Mendelian stage, and where genetic studies are needed as an urgent completion of any monographic research? However, his manifest derision of ecology has still some other grounds. He fears the invasion of the ecological point of view into his field. When this invasion becomes more and more urgent, he knows that the period of the Olympian mind is over and fears that the consequent revolution of genetics will rob him of the certainty of conceptions and results which are so satisfactory to him to-day.

In view of these unsatisfactory relations between both sciences we shall try here to underline the importance of genetic research for ecology, and it is hoped that a geneticist may soon try to review the importance of ecological research for genetics.

### 2. HEREDITY OF IMPORTANT ECOLOGICAL CHARACTERS

We shall first turn our attention to a series of genetic facts closely concerning the student of ecology.

Environmental factors commonly influence morphological characters of the organism. The number of facets in the eye of *Drosophila*, the number of bristles on a certain part of this fly, the tail-length of rats, the colour of mammals and insects are decidedly influenced by temperature. Every change in environment may influence the percentage of crossing-over and the mutation rate.

However, fundamental changes in vitality and other physiological functions very often accompany morphological changes, and this is of paramount importance to the ecologist:

1. Longevity is based on genetic constitution. In crossing two strains or races longevity is often longer than in either of the parents. For *Drosophila* Pearl[2] reports:

| *Wild* | *P*<br>*Truncate* | $F_1$ | $F_2$<br>*Tr.* ♂ × *W* ♀ | $F_2$<br>*W* ♂ × *Tr.* ♀ |
|---|---|---|---|---|
| ♂40·5 | 26·9 | 47·8 | 32·8 | 31·1 days of adult life |
| ♀30·5 | 18·5 | 46·6 | 25·9 | 27·3 ,, ,, |

In the 1st filial generation duration of life is considerably longer than in either parent, while in the 2nd filial generation it is intermediate.

The crossing of different races of the parasitic wasp *Spalangia*[3] yields:

| | *Longevity of* ♀ | *Egg-production of* ♀ |
|---|---|---|
| *Spalangia orientalis* . . | 15 | 75 |
| *S. sundaica* . . . | 27 | 170 |
| *S. or.* ♀ × *S. sund.* ♂. . | 30–2 | Up to 240 |

2. *Spalangia* also served as an example of constitutional change of fertility. In *Bruchus quadrimaculatus*[4] similar observations have been made on different mutations.

| *Phenotypic colour* | *Eggs per pair* | *Per cent. hatched* | *No. of pairs* | | *Index of total fertility (100 pairs)* |
|---|---|---|---|---|---|
| | | | *Fertile* | *Sterile* | |
| Wild . . | 90 | 70 | 70 | 0 | 6,300 |
| Red . . | 48 | 80 | 70 | 0 | 3,840 |
| Red maculated . | 42 | 80 | 70 | 0 | 3,360 |
| Black . . | 40 | 80 | 70 | 0 | 3,200 |
| Grey . . | 13 | 35 | 36 | 34 | 514 |
| Wild ♀ × grey ♂ | 18 | 69 | 11 | 10 | 524 |
| Grey ♀ × wild ♂ | 24 | 44 | 21 | 0 | 1,056 |

Tenenbaum[5] has recently demonstrated for the Palestine race of *Epilachna chrysomelina* that reduction in size of a system of elytral spots goes parallel with heavy depression in vitality and fertility, being therefore an easy indicator of far-reaching physiological reconstruction of the body.

Homozygotic grey-coloured Schirazi Caracul sheep are always lethal in the first year after birth. Physiological disorders in connexion with lab-ferment secretion are connected with this mutation.[6]

3. Length of development is also influenced by constitutional changes. In *Ephestia kühniella*[7] in the mutations 'red eyed' and 'black scaled' the following statistically significant differences have been observed:

| *Mutation* | *Duration of development* | $M \pm 3\,m$. |
|---|---|---|
| Black eyed . . . | 90·8 days | 90·3–91·3 days |
| Red eyed . . . | 92·5 „ | 91·7–93·3 „ |
| Wild coloured . . | 87·6 „ | 87·1–88·1 „ |
| Black scaled . . . | 86·5 „ | 85·8–87·2 „ |

4. Every change in constitutional vitality has far-reaching consequences. In *Drosophila* the stable maximum population to be reached within a stable, closed environment differs with each mutation.[8] Wild *Drosophila* populations stabilized at 938 individuals in a pint bottle, those of the mutant quintuple at 319 only, and those of mutant vestigial at 345.

The wild type is vitally stronger than almost all known mutations. This is confirmed by the fact that in mixed experimental populations of *Drosophila* nearly all mutants are eliminated by the wild form after a very few generations.[9]

5. Herter[10] has shown that the preference temperature of mice is also subjected to Mendelian heredity.

6. Genetic constitution is also connected with disease resistance, e.g. as Gowen[11] has demonstrated in strains of mice. The constitutional part in survival was after inoculation of pseudorabies in various strains:

S. 8·4%; Wf. 55·4%; Ba. 11·5%; Sch. 22·6%; sil. 52·2%.

A few of the recent researches on mutability demonstrate the importance of co-ordinated ecological research. The frequency of mutation in nature seems to fluctuate, but not seasonally. The table on p. 148 shows Spencer's[12] observations in different species of *Drosophila*.

It is still unknown as to which environmental factors may influence or inhibit those mutations. Cosmic radiation is probably much too weak to have any influence on them.[13]

We have mentioned before that mutation-rate is influenced by temperature, but the rate at which mutability rises is about twice as great as that of speed of development (except in highly mutable genes).[14] Other factors as well as chemical stimulation or exposure to radiation, &c., also may increase the mutation-rate or perhaps even mutation-tendency. In radiations, wave-length has almost no influence, but the frequency of mutations is proportional to the dosage, regardless whether this dosage has been given in a high or low concentration (i.e. quickly or slowly) with or without interruptions. Whereas the presence of most genes within the cell is obligatory in all stages of development, their specific influence on certain processes or periods of development is often effective within a limited period only. This is not always the case.

| *Length of period* | *No. of mutations* |
|---|---|
| 28th month | 25 |
| 35th „ | 29 |
| 38th „ | .. |

In glass-winged *Ephestia*-moths part of the wing-area loses its scales.[15] Position and extent of the areas as well as percentage of individuals showing this character depend mainly on temperature. High temperature increases the extent of 'glass-wingedness', but it is of no consequence whether the exposure has taken place at the end or at the beginning of development.

Sensitive periods occur for certain characters in normal development probably oftener than is realized to-day, perhaps because normal development has provoked special research in this respect to a smaller degree. But the response of quite a series of mutant characters to external stimuli (e.g. temperature) is certainly different in different stages of development. In *Drosophila* such results have been obtained for characters as short wing, scute-l, mottled-eye, vestigial, &c.[14]

The knowledge of lethal genetic combinations is often useful for the understanding of sudden population changes as a consequence of changed sex ratio or changed fertility. It is important to know that almost every mutation is a minus mutation, lowering the general vitality and often the fertility or other important processes. Selection in combination with the conservatory forces of heredity tends to maintain a population genetically stable in any given habitat, as long as its environmental factors remain more or less constant. The chance that vitally potent mutations may develop and form new species is almost only a question of the length of geological periods. This has been clearly demonstrated by Kinsey[16] for North American Cynipidae.

## 3. THE INTERACTION OF ENVIRONMENT AND HEREDITY IN THE DIAPAUSE

A good illustration of the coaction of hereditary as well as environmental factors is the phenomenon of diapause. We shall here restrict the term diapause for any case of dormancy, interrupted development or maturation, which is not immediately broken by the change of unfavourable into favourable external conditions. Hibernation as displayed by the Mexican bean beetle, broken by contact humidity and beyond a certain temperature-threshold, is not a diapause, whereas the hibernation of the eggs of *Bombyx mori* is.[17, 18]

There exist a series of animal species which continue to develop uninterruptedly as long as they are under favourable conditions. Besides many homoiothermous animals (voles, mice, &c.), flies like *Lucilia*, *Phormia*, *Calliphora*, gnats like *Phlebotomus*, wasps like *Hormoniella*, and many other insects belong to this group. Cousin[19] has conclusively demonstrated that Roubaud's theory[20] of cyclic self-intoxication by urates after a sequence of generations, followed by an obligatory dormant period of purgation, is entirely baseless. Development is continued uninterruptedly as long as optimal conditions prevail, and diapause occurs as soon as one of the important environmental factors (food, temperature, humidity, population density, &c.) falls below a certain threshold of tolerance. The percentage of individuals entering diapause depends upon the age-distribution of the population (determining the number of individuals being in the sensitive age) and on the degree of unfavourableness of the factor or factors concerned. In this common case heredity has no part in the diapause, except in determining potential diapause as part of the normal reaction-base.

The reverse is true for another series of phenomena, rather common in the moderate climates of the Holarctic kingdom. Most birds and mammals with a seasonal rutting-period (e.g. goat, sheep, sparrow) and many insects with one annual generation only (*Bombyx*, *Lymantria*, *Cimbex*, &c.) belong here. Diapause sets in at a fixed stage of development independent of all possible environmental conditions, from optimal to almost intolerable, and is not broken even in favourable conditions until a certain period of time has passed. Under unfavourable conditions the diapause may last much longer, eventually until death sets in. The awakening from the diapause occurs in this case simultaneously in the laboratory and in nature. We have seen this often in *Cimbex humeralis* and *Eurytoma amygdali* in Palestine.[21] In those cases hereditary diapause overrules all ecological influences.

It is still entirely unknown as to how this timing of the diapause is regulated, especially as it almost always leads to a very 'utile' synchronism between the optimal conditions of food, climate, &c., and the active period of the animal concerned. In certain cases, at least, the timing is not conditioned by time. Goldschmidt has shown for the egg of *Lymantria dispar*[22] and Bodine for those of *Melanoplus differentialis*[23] that the development inhibition of the egg is broken by low temperatures and that hatching depends on the sum of effective temperatures after the breaking down of the diapause. Winter cold is a regular phenomenon in the natural environment of these species, and Goldschmidt[22] is even inclined to conclude that every population (or race) of *Lymantria* is fitted genetically in the special climatic cycle of its natural habitat by small hereditary changes in the degree of cold necessary for breaking the diapause and in the thermal constant.

Between those cases appearing to be wholly determined by hereditary or environmental factors occur many stages of transition in nature, where the coaction of both is very obvious. Dawson[24] has shown for *Telea polyphemus*, Bacot for rat fleas[25] that a certain percentage of offspring grows dormant or develops parallel to the fall or rise of temperature during a certain sensitive period of previous development. This means that under certain conditions all eggs may become dormant. But under abnormal climatic conditions, e.g. with ascending temperature in autumn, some of the pupae, &c., go into dormancy anyhow, whereas others emerge under these favourable conditions. This bimodal curve is decidedly genetically determined. But in the climate of Minnesota, favourable conditions in autumn lead the developing moths or their offspring to a premature death in winter. The obligatory partial hereditary diapause is therefore of vital importance to the maintenance of the species, whereas the partial facultative emergence would eventually open new developmental possibilities under other climatic conditions.

In some species, as in *Bombyx mori*, we find races with a different number of annual generations even in the same habitat. If more than one generation is present, one or two are of the emergent, one invariably of the dormant type. Foa[18] attempted to correlate the voltinism of the silk-worm with the influence of ascending or descending temperatures on the early stages of the maturing egg, inducing the appearance of large or small cells in the germinal stripe.

Very complicated hereditary conditions affect the diapause of pupae of *Deilephila euphorbiae* near Lwow, as studied by Heller[26] (see table on p. 152).

Types 1, 2, 4, 5 are certainly genetically conditioned, 3 and 6 may be extremes of types 2 or 5 only. In types 7 and 8 it is difficult to ascertain whether lethal hereditary characters or individual cases of disease are the reason for the occasional appearance of these groups. Groups 2 and 5 predominate, as a rule, which also results in a bimodal curve. But more than one character is concerned in the determination of pupal diapause of *D. euphorbiae*, as is clearly demonstrated by the physiological analysis. Induction of emergence or dormancy depends also in this case on environmental conditions (especially temperature).

The varying life-history of the polyphagous egg-parasite, *Trichogramma*, its dependence on the special life-history of its special host, its seasonal cycle and diapause, have been submitted to a masterly analysis by Marchal.[27]

Similar phenomena are by no means unknown in mammals and birds. The seasonal fixation of sexual activity and of the coincident hormonal secretions are one of them. Fig. 25 shows how deeply fixed the seasonal rhythm of the natural habitat, in a group of nearly related gazelles, is in agreement with environment, mainly rains and vegetative period. In the Cairo Zoo where food supply and climate are even throughout the year and where no rainy season occurs at all, this rhythm of the original habitat persists with regard to births.[28]

*Constitutional types of pupal development of* D. euphorbia *at 22° C.*

| *Type* | *Designation* | *Development* | *Loss of weight* | *Smallest $O_2$ consumption per cm.$^3$* | *Highest $PO_4$ per cent. per mg.* | *Reducing substances* |
|---|---|---|---|---|---|---|
| 1 | Biannual | Days<br>640 | Very slow | .. | Up to 70 | .. |
| 2 | Dormant | 270–330 | Slow | 20 | 50–5 | 50 mg. % glucose |
| 3 | Dormant with final loss of weight | During or after winter | Quick | 20 | .. | .. |
| 4 | Protracted | 40–50 | Fairly quick | 35 | ..<br>.. | .. |
| 5 | Emergent | 17–21 | Quick | 50–60 | .. | 50 |
| 6 | Quick emergent | 13 | Very quick | .. | 30 | .. |
| 7 | Soft winged | 3–6 | .. | .. | .. | 220 |
| 8 | Black pupae | After pupation | .. | 160 | .. | 380 |

## 4. THE INTERACTION OF ENVIRONMENT AND HEREDITY IN SEX-DETERMINATION

Sex-determination yields another splendid illustration of coaction between genetical and ecological factors.

The discovery of the sex-determining *x* and *y* chromosomes in every living plant and animal by McClung, Wilson, Montgomery, and others, at the beginning of this century, and its confirmation by the mono-sexualism of the offspring

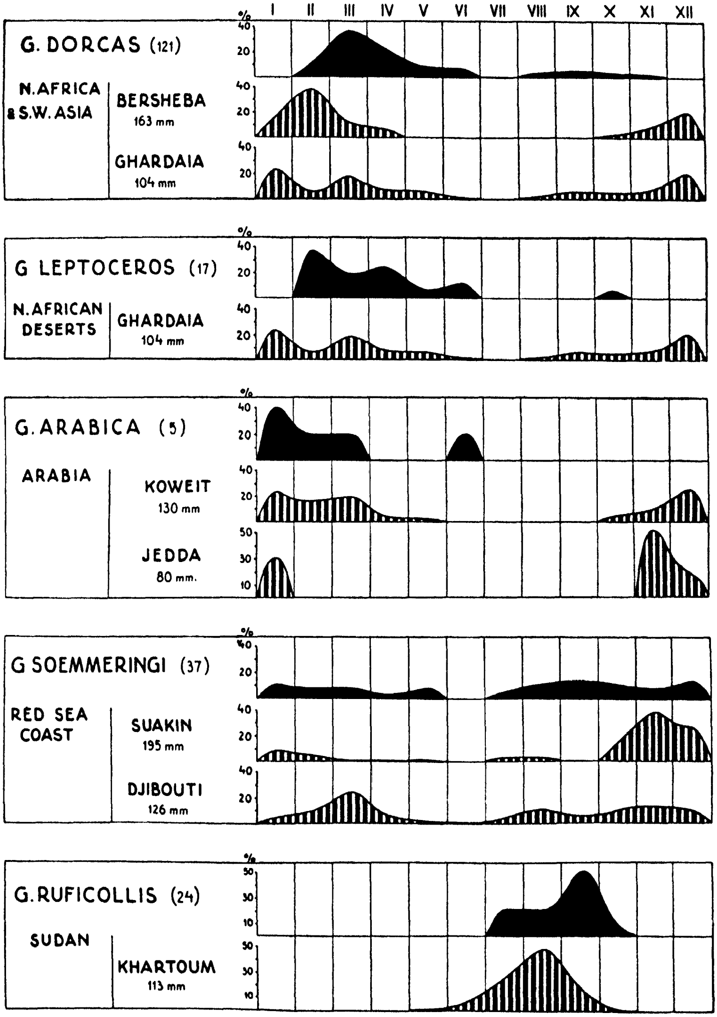


Fig. 25. Correlation between monthly percentage of births of some gazelles in the Cairo Zoo (with optimal and equal feeding throughout the year—as reported by Flower) with the rainfall in their natural habitat.

of the one egg-polyembryonism in the armadillo *Tatusia*,[29] the chalcidid wasps *Encyrtus* and *Ageniaspis*, the different chromosome structure in both body halves in bilateral gynandromorphs, &c., seemed to furnish a decisive and definite defeat to any theory considering any environmental influence whatsoever on sex-determination.[30, 31]

However, whether we like it or not, there is no doubt that quite a series of well-known facts are not easily explained by the orthodox chromosome theory. One of the most convincing is the fact that most organisms still seem to contain the potentialities of both sexes. This is certainly true for habitual hermaphrodites such as most earth-worms, snails, and tapeworms; for cyclic hermaphrodites, producing alternately sperms and ova as in *Ostrea edulis*,[32] or in successive hermaphrodites producing first sperms and later on eggs only, as in *Icerya purchasi*.[33] Steinach's experiments on feminization or masculinization of the opposite sex in secondary sexual characters, as well as in behaviour, by castration followed by transplantation of the opposite sex glands, are a further proof for these potentialities.[34] Most convincing are the experiments with poultry or pigeons. When the developed ovary of a hen, the left one, is operatively removed, the right ovary, suppressed and undeveloped hitherto, begins to swell. It then develops not into an ovary but into a normally functioning testis, producing sperms as well as internal secretion. In consequence, the whole exterior of the hen, as far as it is based on secondary sexual characters, changes into that of a cock. Even the uterus and vagina may change to such a degree that these individuals are able successfully to fertilize normal hens.[35]

In the amphibians Bidder's organ probably always develops into a half-functioning ovary. If the testes are exstirpated in the males of *Bufo viridis*, the individuals become normal ovipositing females. The lability of amphibian sex-glands during the early development is a long and well-established fact. Witschi obtained from tadpoles of *Rana silvatica*, bred at high temperatures, or from eggs which were over-matured experimentally, male frogs only.[36]

Most impressive are the experiments of Baltzer and others with the marine worm *Bonellia viridis*.[37, 38]. Male larvae grow into females, if they have no opportunity to settle on and suck the pharynx of an adult female. If female larvae settle on and suck the pharynx of an adult female they change into males. Chemicals, such as weak solutions of copper-sulphate, also have a sex-determining effect. Intersexes developing from female larvae which have not sucked sufficiently long on the pharynx of an adult female are known. After a certain period of attachment all these larvae grow into males.

We learn that in *Daphnia* environmental conditions during a critical period of egg-development determine the chromosome character and therewith the sex.[39] Among these environmental conditions the size of the life space has an important influence. This important fact is confirmed in other groups, e.g. in Ichneumonidae or in Mermithid worms:

*Sex of* Paramermis contorta *in chironomid larvae*[40, 41]

| *No. of parents per larva* | *No. of females* | *No. of males* | *Ratio of female/male* |
|---|---|---|---|
| 1 | 255 | 17 | 15·00 |
| 2 | 180 | 106 | 1·14 |
| 3 | 47 | 82 | 0·57 |
| 4 | 23 | 41 | 0·56 |
| 5 | 5 | 25 | 0·20 |
| 6 | 3 | 15 | 0·20 |
| 7 | 3 | 11 | 0·27 |
| 9 | 1 | 8 | 0·13 |
| 10 | 4 | 26 | 0·15 |
| 11 | 2 | 9 | 0·22 |
| 17 | 2 | 15 | 0·13 |

Population pressure leads to strong prevalence of the male sex.

This type of sex-determination leads to another ecologically important case. Many animals reproduce parthenogenetically for a series of generations, producing sexual generations during certain seasons. Weismann and others attempted to explain these changes, which occur in aphids, Cladocera, and rotifers as genetically induced. Observations extending over long years, combined with laboratory experiments, showed that under optimal conditions these animals may reproduce by parthenogenesis indefinitely and that the appearance of the sexual part of the cycle is always induced by unfavourable environmental conditions. The work of Luntz[42] and Wesenberg-Lund[43] on rotifers, the research on Cladocera,[44] the behaviour of aphids[45] in tropical and subtropical countries, prove these descriptions to be true, as do also the recent investigations of Hartmann, Klebs, &c., on fresh-water protists, in which unfavourable environmental factors were found to induce depression connected with conjugation.

Environmental factors induce the appearance of males in the sexual cycles, environmental factors (temperature) induce the alternating sperm and egg-producing cycle of the oyster. Environmental factors induce the male sex in frogs (temperature, maturity of egg), in *Bonellia* (chemical stimuli), in Mermithids (density). All these facts are not explained by differential mortality of both sexes in early stages of development, an explanation which is often and probably correctly used for the unequal sex-ratio in man. All facts recorded here are incompatible with the conception of the sexes as two different qualities of the living matter definitely determined by chromosome pattern. They are intelligible when sex is considered as a form of polar differentiation of the same quality. And all modern theories, which consider the intersexes too, start from this point of view.

There exist still purely morphological theories, as that of Bridges,[46] which tries to explain the sex as a numerical relation between *x*-chromosomes and autosomes in *Drosophila*:

| *Sex-condition* | *No. of x-chromosomes* | *No. of autosomes* | *Ratio autosomes/ x-chromosomes* |
|---|---|---|---|
| Over-females . . | 3 | 2 | 0·67 |
| Females . . . | 4 | 4 | 1·00 |
| " . . . | 3 | 3 | 1·00 |
| " . . . | 2 | 2 | 1·00 |
| Intersex . . . | 2 | 3 | 1·50 |
| Male . . . | 1 | 2 | 2·00 |
| Over-male . . | 1 | 3 | 3·00 |

In the physiological theory of sex-determination of Goldschmidt[47] Mendelian intersexes occur regularly when crossings are made between certain races of *Lymantria dispar*:

| *Crossings* | *Results* |
|---|---|
| Hokkaido ♀ (weak) × Hokkaido ♂ (weak) | Only purely monosexual offspring. |
| × European ♂ (less weak) | Only purely monosexual offspring, but eventually weak intersexes. |
| × Gifu ♂ (medium) | Heavy intersexes. |
| × Ogi ♂ (strong) | Eventually only male offspring. |

We have here a similar quantitative series without correlated changes in chromosome ratios. Goldschmidt assumes that male and female potentialities are present in every body, both being present in certain intensities (♂ 120, 100, 80; ♀ 100, 80, 60). If the difference of both intensities is at least 20 units, pure sexes are produced, whereas slighter differences induce the appearance of intersexes. The beginning of the reaction determines the degree of intersexualism. Goldschmidt conceives, therefore, that the sex-genes are connected with intensity differences.

Riddle[48] leaves the chromosome base of sex-determination still farther behind, in stating that in eggs of frog, toad, or pigeon all conditions which increase the oxidation rate favour the tendency towards male, all those which decrease it favour the female tendency. In vertebrates the male sex has constantly a higher intensity of metabolism (5–14 per cent.). The lipoid content of blood is lower in males than in females, therefore metabolism is higher in the former, as is known for microgametes in Protozoa. For locusts and some other insects the author can confirm that metabolism is always higher in the male sex (related to the weight-unit). This would mean that the *x*-chromosome does not determine the sex, but the general intensity of metabolism, which in turn determines the sex. This agrees with studies on metabolism of the oyster, which is quantitatively different in both sexual phases. And we have no difficulty in understanding that metabolic intensity may be changed by environmental influences. This change of metabolic intensity leads to a physiological as well as structural and behaviouristic reconstruction of the body, accompanied by change of sex.

We can thus conclude, with regard to the problem of sex-determination alone, where the uncompromising spirit of strict geneticism has won decisive victories, that it provides a good illustration of the coaction of heredity and environment within the organism.

### 5. THE INTERACTION OF ENVIRONMENT AND HEREDITY ON GEOGRAPHICAL VARIATION

Geographical variation is the change of certain characters, transitory as a rule, within one species, with the shift of its habitat within its range of distribution. Whereas a few species of a very large area, as the Painted Lady (*Vanessa cardui*), show almost no variation, in most animals changes occur in individuals from the eastern or northern end of their area to the western or southern border. The transition is gradual and the variation ranges of two neighbouring areas overlap as a rule. This holds for changes in size, colour, morphology of certain organs, &c. Fig. 26 illustrates this point.[49, 50]

A further very common trait of geographical variation is the simultaneous shift in a series of characters.

The large woodpecker (*Dryobates major*) is represented by two forms in central Europe:[49] the western form *D.m. pinetorum* and the eastern race *D.m. major*. These differ in the following characters:

| *Character* | *D.m. major* | *D.m. pinetorum* |
|---|---|---|
| 1. Length of wing . . | 136–145 mm. | 131–138 mm. |
| 2. Length and width of eggs . | 26·9 × 20·7 | 25·7 × 19·3 |
| 3. Ratio wing length/beak length . . | 20·6 | 22·0 |
| 4. Form of beak . . | Slender, steadily becoming narrower | Remaining thick, broad from base to middle of beak |
| 5. Colour of lower side . | Mainly white | Mainly light brown |

Five characters, at least four of which are heterogeneous, show a simultaneous and steady alteration with territorial shift. Extended correlated alteration of morphological and physiological character has been described by Goldschmidt[51] for the caterpillars of *Lymantria dispar*.

This modification of characters is certainly not a uniform phenomenon from the genetical point of view. There are characters which seem to depend mainly upon the intensity of certain environmental factors, and there are others which most probably are independent of such influences.

The first group often leads to phenomena commonly regarded as adaptive. The few fundamental general rules of zoogeographical variation belong to this group.

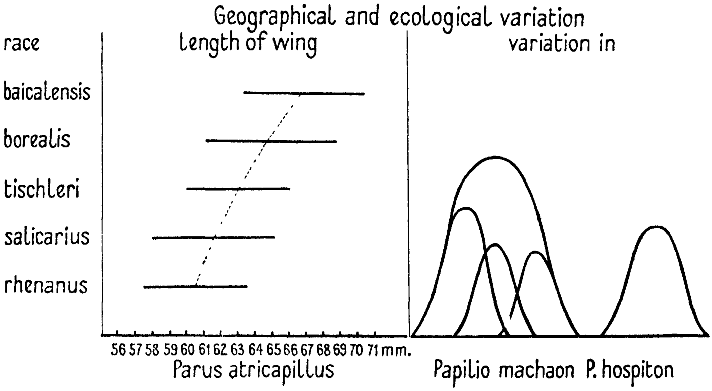


FIG. 26. Geographical variation. A. Range of variations in wing length of geographical races of *Parus atricapillus* (in mm.). The dotted line connects the average values. (After Rensch.) B. Variation (ecological and geographical) in the Swallowtail, *Papilio machaon*, as compared with variation of the same character in a closely related species, *P. hospiton*. (After Eller.)

Bergmann's[52] rule states that races of mammals and birds living in different climates increase slowly in size towards the colder habitats of their area. Cold delays sexual maturity, which is—also relatively—accelerated by high temperature. The period of growth is lengthened. The cell size remains constant, but the number of body-cells increases in consequence of this prolonged period of growth. This simultaneously induces a smaller surface/volume ratio in colder climates, economizing thus the loss of heat by radiation.

The same influence of temperature on the growth is often met with in poikilothermous animals (snails, amoebae, &c.), but any other factor may interfere with this tendency. Unfavourable conditions of humidity, of food, lime content of soil, &c., immediately reduce the size, thus interfering with the mere temperature influence. Many positive observations on this have been compiled by Hesse[53] and Rensch.[49]

Allen's rule: Under different climatic conditions races of mammals and birds show a considerable reduction in the relative and often in the absolute size of body projections, such as tail, ears, and extremities, towards the colder habitats.[54]

In the American woodpecker *Dryobates villosus* the relative wing length[49] is reduced in the north.

| *Race* | *Area* | *Total length* | *Wing length* | *Relative wing length* |
|---|---|---|---|---|
| *D.v. septentrionalis* | Canada, Montana | 248 | 132 | 53 |
| *D.v. leucothorectis* | Arizona, New Mexico | 216 | 126 | 58 |
| *D.v. extimus* | Costa Rica, Panama | 172 | 103 | 60 |

The reduction of ear-size in hares towards the north has been quoted by Hesse[53] and others. It is probable that exposed body parts suffer from growth inhibition, reduction of vascular system, &c., as a direct consequence of exposure to cold. Under the influence of cold these thin and exposed parts anyhow show a temperature far below that of the body. A few examples exist also with regard to insects. But the mouth parts of the honey-bee grow smaller in warmer climates:[55]

| *District* | *Tongue length* |
|---|---|
| Orel district (Central Russia) | 6·73 mm. |
| Ukraine | 6·549 „ |
| Italy | 6·234 „ |
| Palestine (Jerusalem) | 6·292 „ |

Gloger's[56, 49] rule: The melanins of mammals, birds, and of perhaps all animals intensify with increasing temperature and air humidity. Heavy melanin accumulation in bird feathers leads to the appearance of interference colours. Dry, hot weather increases the phaeomelanins only, leading to yellow desert-coloured degrees of oxidation, whereas the eumelanins disappear. Strong cold inhibits first the formation of the phaeo-, later of the eumelanins resulting finally in the 'white' polar coloration.[57] The thorough knowledge of coloration in one group may enable a fair climatic description of the natural habitat of any race. Hinton [58] says with regard to the African squirrel *Heliosciurus rufobrachium*: 'When one knows how to read the characters of this squirrel one can describe the physical condition of the locality from which any given specimen came without knowing either the name or the whereabouts of the locality.'

Many other rules can easily be formulated. But it seems inadvisable to do so without a thorough revision of the relating facts. Several of such rules state:

Fur and feathers of mammals and birds grow thicker in colder climates.

Tropical birds lay fewer eggs than the same species in a moderate climate (perhaps owing to the shorter length of day in the tropics).[49]

The relative heart-weight of birds and mammals increases in the same species with increasingly colder climate, &c.[53]

The characters concerned in these three rules are all hereditary. But convergent phenogenetic characters may be produced in the experiment. Sumner[59] bred genetically equivalent lots of mice at different temperatures with the following results (after 2 months):

| *Temperature* | *Weight* | *Length of* *Tail* | *Length of* *Ear* | *Length of* *Hind foot* | *Weight of hair of fur* |
|---|---|---|---|---|---|
| 26·3° C. | 17·0 g. | 93·2 mm. | 16·0 mm. | 21·4 mm. | 264·6 mg. |
| 6·2 | 17·9 | 75·9 | 15·9 | 20·9 | 294·8 |

The same holds good for insects, as was demonstrated by the classical experiments of Standfuss,[60] who obtained in Switzerland from local pupae of *Vanessa antiopa*, kept in cold, the Arctic form of this species; and from local pupae of the Swallow-tail *Papilio machaon*, kept at high temperatures, the Palestine form of this butterfly.

In discussing the importance of the 'Dauermodifications' for hereditary fixation, the time factor should not be overlooked. If a species may 'remember', so to speak, for some time after they have ceased to act, external stimuli, which, as in the experiment, have worked for a few generations only, how much deeper should be the fixation of this memory after the stimulus has worked for secular or even minor geological periods?

It does seem logical to assume that many of these hereditary geographical races originated as phenovariants, which became genetically fixed under the constant and equal influence of climatic factors through many generations.[49]

Connected with this conception is the Dauermodification of Jollos.[61] Under the influence of environmental conditions certain characters of an organism as well as of a population change. This change is reinforced or retained as long as the inducing external conditions continue. When they cease and the normal environment is restored, the change of character is retained for some period and will continue to appear in a gradually decreasing degree still for some generations until it finally disappears.

*Induction of half-moon formation in* Arcella polypora *by selection*

| *No. of selection* | *Date* | *A*<br>*Under normal cultivation* | | | | | *B*<br>*At environment favouring half-moon formation* | | | | | *Remarks* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 0 | 1 | 2 | 3 | 4 | 0 | 1 | 2 | 3 | 4 | |
| 0 | 30.x.22 | .. | *1* | .. | .. | .. | .. | *1* | .. | .. | .. | Selection of plus variants. A. Under normal cultivation. B. Under conditions favouring half-moon formation. The nos. from 0 to 4 describe the different stages of half-moon formation from normal (0) to complete (4). |
| 1 | 8.xi.22 | 75 | 219 | 6 | .. | .. | 22 | 203 | 56 | 19 | .. | |
| 2 | 16.xi.22 | 24 | 267 | 7 | *2* | .. | 5 | 107 | 101 | 87 | | |
| 3 | 27.xi.22 | 5 | 207 | 59 | *29* | .. | .. | 9 | 98 | 164 | *29* | |
| 4 | 5.xii.22 | .. | 82 | 101 | *117* | .. | .. | 2 | 7 | 86 | 205 | |
| 5 | 13.xii.22 | .. | 34 | 113 | 144 | *9* | .. | .. | .. | 12 | *288* | |
| 6 | 22.xii.22 | 1 | 24 | 68 | 186 | *21* | .. | .. | .. | 3 | *297* | |
| 7 | 3.i.23 | .. | 10 | 7 | 75 | *208* | .. | .. | .. | .. | 300 | |
| 8 | 15.i.23 | 6 | 11 | .. | 80 | *203* | .. | .. | .. | .. | .. | |
| 9 | 25.i.23 | .. | .. | 2 | 43 | 255 | .. | .. | .. | .. | .. | |
| 10 | 5.ii.23 | .. | .. | .. | 21 | 279 | .. | .. | .. | .. | .. | |
| 11 | 25.ii.23 | .. | .. | .. | 8 | 292 | .. | .. | .. | .. | .. | |
| 12 | 1.iii.23 | .. | .. | .. | .. | 300 | .. | .. | .. | .. | .. | |
| | 5.vii.23 | .. | .. | .. | .. | *1* | .. | .. | .. | .. | .. | Beginning of selection: breeding in order to obtain minus variants in normal cultivation. |
| | 15.vii.23 | .. | .. | .. | .. | *300* | .. | .. | .. | .. | .. | |
| | 24.vii.23 | .. | .. | .. | .. | *300* | .. | .. | .. | .. | .. | |
| | 31.vii.23 | .. | .. | .. | .. | *300* | .. | .. | .. | .. | .. | |
| | 12.ix.23 | .. | .. | .. | *14* | 286 | .. | .. | .. | 13 | 287 | |
| I. | 22.ix.23 | .. | .. | *8* | 59 | 233 | at normal environment | | | | | Breeding by selection of minus variants in normal cultivation. (B. without selection.) |
| II. | 13.x.23 | .. | *26* | 95 | 139 | 40 | | | | | | |
| III. | 20.x.23 | *1* | 213 | 66 | 15 | 5 | .. | 82 | 32 | 76 | 110 | |
| IV. | 27.x.23 | *24* | 262 | 14 | .. | .. | .. | .. | .. | .. | .. | |
| V. | 5.xi.23 | *259* | 41 | .. | .. | .. | .. | .. | .. | .. | .. | |
| VI. | 12.xi.23 | *300* | .. | .. | .. | .. | 113 | 109 | 16 | 47 | 15 | |
| | 15.xii.23 | .. | .. | .. | .. | .. | 210 | 57 | 12 | 11 | 9 | |
| | 14.i.24 | .. | .. | .. | .. | .. | 272 | 16 | 4 | 6 | 2 | |

Similar Dauermodifications are known for toxin-habituation in Ciliata as well as for some Metazoa.(h) The most plausible interpretation of these facts is that the modification is based on cytoplasmic changes, induced by the environment, which only gradually overcome the action of those genes normally controlling the modified character. Cytoplasmic influence has for some time already overcome the directing influence of gene-constitution by 'mnemic' perseverance, which means that environment does not simply release the phenotypification of genes, but influences the mechanism of release decisively by modifying the protoplasm.

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(h) See note h, p. 180.

There are other characters, as the genitalia of most insects, which show rich geographical variability without recognizable parallelism between any environmental factor and variation tendencies.

We are far from understanding conclusively as to how the genes within the chromosomes, mutations, Dauermodifications, and environmental influences coact. There is little doubt that most of what we call geographical variation is some type of Dauermodification within the range of a specific reaction basis or constitution. In *Papilio machaon*,[50] in *Lymantria dispar*,[51] and in some other cases this has been demonstrated clearly not to be the case. But these negative results should not be understood to exclude geographic variation in all cases and to be the only way of species formation. Cases of transition of monophagous insects to new hosts and subsequent isolation of two biological races (*Carpocapsa pomenella* and *Rhagolatis pomonella* in North America), which have not yet been analysed by the geneticist, are possibly beginnings of species formation.

We now leave this topic without trying to understand the way of formation of new species. The material at hand is still utterly inadequate to approach a solution. But we would like to point out that different ways, and not one, are realized for this purpose in nature. Sudden high mutability induced by extrinsic as well as by intrinsic factors, directed, but probably more often quite undirected; permanent plasmotic fixation of phenotypical reactions of which the Dauermodification seems to be a first step—these and still other ways are all probably verified occasionally.

## 6. THE PROBLEM OF ADAPTATION

Finally, we shall deal with the problem of adaptation. Some of the rules of geographical variation, expressing direct parallelism between tendency and intensity of variation as induced by certain environmental factors, are regarded as adaptive ones. In an earlier stage of biological development these were considered as the result of selection among mutants. But it has been repeatedly pointed out that most of the animals and birds of the desert showing extreme desert colouring are nocturnal, i.e. would not benefit at all from the 'protective' colouring, whereas some of the diurnal species of the same habitat are black, i.e. very conspicuous. Heim de Balsac[64] has recently shown that the hypertrophic development in the auditory bulla in desert mammals is a common result of the influence of desert conditions, and that no plausible hypothesis as to its physiological importance could be suggested. In polar animals the white colour might be of selective importance and probably is so occasionally. But the tendency to white colouring by inhibition of melanin development in cold remains a primary fact. The same is true for the wingless insects of all classes in the Kerguelen Islands.[65] The strong winds are certainly unfavourable to the maintenance of weak fliers with large appendages, i.e. with great surface resistance. However, cold induces short-wingedness by inhibition of tyrosinase development, as has been shown experimentally by Dewitz.[66] And results of field- as well as laboratory-research in plants lead to the same conclusions:

> 'Of approximately a hundred species employed in adaptation studies, none has failed to respond to intensity or duration of factor stimuli, and so uniformly in nature and extent as to leave little doubt that adaptation in plants at least is a universal process, and not a selection of genetic strains or variations. This is indicated likewise by the different types of material, no species having yet been discovered in which the clones differ from the adult individuals in the response to the various factors.'[67]

The agreement observed between form and function is the main reason why most palaeontologists and comparative anatomists are inclined to describe heredity of acquired characters as a 'postulate of the practical reason'. The recent research of Boeker has shown in many cases the extent of the morphological reconstruction of the whole body when a species leaves the normal habitat of its group and lives in a very different environment.

The Rallid bird *Heliornis fulica* of Brazil left the habitat of its nearest relatives in swampy primeval forest and became aquatic, adopting diving habits. Fig. 27 shows how this type of living has influenced the construction of the body. Relics of the land habitat are seen in the long neck and head, the long feathers on wing and tail, the strong development of breast musculature. Adaptations to the water habitat are the lobed toes, the short legs, the strong thigh musculature, the broad hip, the rich fat-deposit in the skin, the large size of the rump gland. Some measurements, related to a size of 20 mm. body-length, are given on the next page.[68]

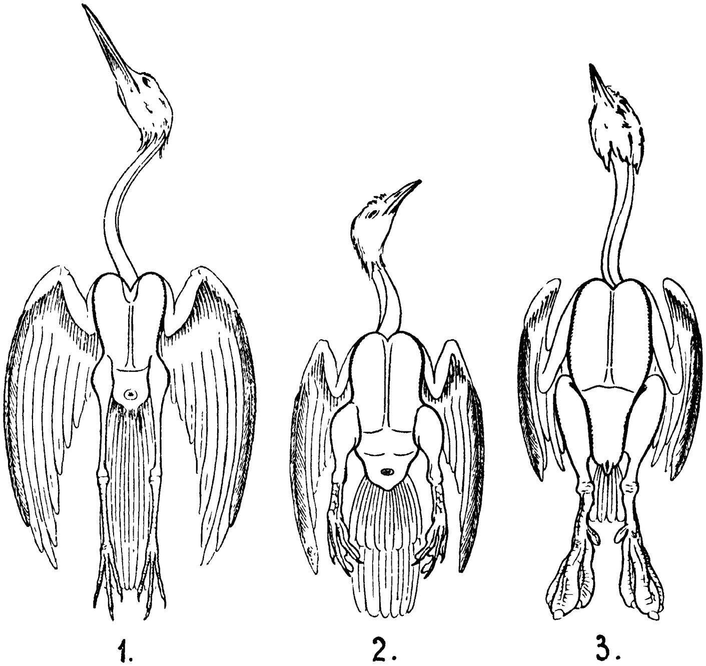

Fig. 27. Ventral view of 1. *Eurypyga helios*; 2. *Heliornis fulica*; 3. *Podilymbus podiceps* from Brazil. (After Boeker.)

The change of manner of life has obviously caused a change of body construction which gives to the Rallid *Heliornis* the appearance at first sight of a true Podicipid.

In studying certain organs of animals we find a surprising coincidence between the form and construction of this organ and the general mode of living of the species.

Dor[69] has recently studied the morphology of the mammal tail in connexion with locomotion. The tail is a splendid object for such studies as it is not a vital organ as regards internal physiology and shows a high degree of variability with regard to osteology, myology, integument, and general form. The degree of relation between development, form, and function of the tail and the mode of living of mammals is surprising. Dor has never met with two species of the same habitat and type of locomotion which were principally different with regard to tail structure. On the contrary, many cases may be quoted where related species had very different tails when living in different habitats or having a different type of locomotion.

| *Habitat* | *Forest swamps* | *Swimming and diving in water* | |
|---|---|---|---|
| Family | Rallidae | Rallidae | Podicepidae |
| Species | *Eurypyga* | *Heliornis* | *Podilymbus* |
| Length of shank, mm. | 18 | 7·5 | 4·5 |
| Length of rump gland, mm. | 2·6 | 7·5 | 6·7 |

> 'The changes of the morphology of the caudal appendage are due to —sometimes delicate—modifications in the animal's way of living. Evidently the caudal appendage, having no determined and constant role, cannot be considered as a factor able to enforce, on its part, the mode of living. On the contrary, it is the tail which adapts itself to the biological conditions of the animal, especially to its mode of locomotion, the main expression of its activity.'[69]

Hesse[53] in his classical book *Tiergeographie auf ökologischer Grundlage* describes an overwhelming number of morphological changes in animals which occur parallel to changes in certain environmental factors. The form of cross-section in fish living on the bottom (in dorso-ventral position, flat), in quiet water (flat laterally), and in running water (round) may be quoted. Convergent development of certain characters as reduction of eyes, lengthening of extremities and antennae, loss of pigmentation in cave and subterranean animals is another illustration.

However, it is unwise to exaggerate the value of these convergencies. Rabaud[70] points out that the 'adaptations' are by no means as ideal as is often claimed. Palmated feet in water-birds are by no means in direct parallelism to swimming power. Whereas the slow and poorly swimming swan has very complete palmate feet, there are only small lobes on the feet of the coot (*Fulica atra*) which is a quick and strong swimmer. *Rallus aquaticus* and *Gallinula chlorops* have free toes, but swim well, whereas many ducks with well-developed webs are poor swimmers. Furthermore, palmated feet are developed in many terrestrial birds of different families (*Columba palumbus*, *Phasianus colchicus*, *Caccabis saxatilis*, *Caprimulgus europaeus*). This means, however, that from the point of view of the palaeontologist or comparative anatomist not all organs are liable to be reconstructed to an equal degree.

Another series of facts deserves our attention, such as the formation of new races by change of host or by host-specialization.[71] Only a few experiments and observations will be quoted.

Plant-feeding Nematodes prefer, as a rule, to feed upon the same host species or even variety upon which their parents have lived. This preference increases with the number of generations a population lives on it, the Nematode thus getting more and more specialized on this particular host. The injury inflicted to the host from a specialized strain is correspondingly more serious than that caused by a generalized strain. 'Finally the specialization may reach such a high degree that even new hosts of the closest taxonomical, physiological, and chemical relationship to the old host are attacked no more or very lightly.'[72] The probability of successive selection among mixed Nematode populations has become rather small with the progress of experimentation. Fig. 28 illustrates a rather interesting phase concerning one of the oldest experiments with *Heterodera schachtii*.

Man has witnessed the invasion of walnut in California by the codling moth (*Carpocapsa pomonella*), both races, that living on walnut and that on apple, being now definitely unable to develop on the respective host of the other variety.[73] Forced transition to new host has been repeatedly observed. *Stilpnotia salicis* in Canada had to leave by force its original European host *Populus italica* for the Canadian *P. trichocarpa*.[74]

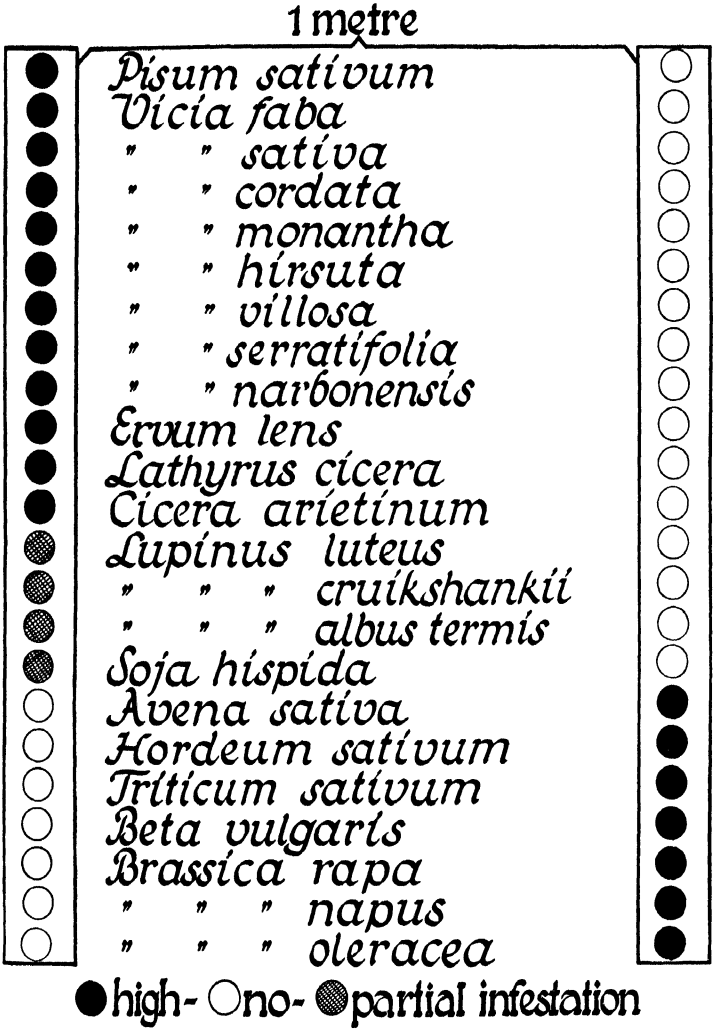

FIG. 28. Diagram to illustrate the experiments of Liebscher (1896) with *Heterodera schachtii.* At left: Plots planted for 13 years with peas and finally highly infested with a strain of *H. schachtii* specialized on peas. At right: Plots planted with oats for 17 years and finally highly infested with a strain of *H. schachtii* specialized on oats. In parallel experimental plots at a distance of 1 m. between them, the following infestation occurred in both plots: black, high; shaded, partial; white, no infestation. (After Steiner.)

The mortality of young caterpillars was heavy in the 1st generations, but normal later on. When retransfer to the original host was tried experimentally the same heavy mortality occurred during the 1st generations.

Harrison [75] produced experimentally a new biological race of *Pontania salicis* adapted to *Salix rubra* from a pre-existing *S. andersoniana* race. Here also initial mortality of the young larvae was high, but after a period of 4 years a flourishing colony was established on the new host. Specimens of *S. andersoniana* were now planted among the other willows, but during 3 subsequent years of observations none of the sawflies showed an inclination towards returning to this plant. Harrison concludes that the modified egg-laying preference had become germinally fixed.

That oligophagous insects often—but certainly not always—tend to prefer for oviposition the host in which they have self-developed is a well-established fact, known as 'the host selection principle'.[76] Such preferences are not always exclusive or alternative ones. Quite commonly only a certain tendency is observed, as in the case of two races of *Hyponomeuta padella* observed by Thorpe.[77] Females of both races were given equal opportunity to oviposit on hawthorn and blackthorn *and* on apples:

| | *Eggs and percentage of total oviposition deposited on* | |
|---|---|---|
| *Moths* | *Hawthorn* | *Apple* |
| Hawthorn race . . | 911 (79·3%) | 237 (20·7%) |
| Apple race . . . | 367 (9·8%) | 3,397 (90·2%) |

The number of eggs was about equal in all ovipositions. Each race preferred its own normal food, but would have taken freely to the alternative host if forced to do so.

After a full discussion of all known cases of biological races in insects and allied groups, Thorpe[71] comes to the following conclusion:

> 'We may say that many of these experiments are easily explained on some form of Lamarckian theory, but extremely difficult to account for on any other lines. If the hypothesis were not such a debatable one the evidence might well be regarded as almost conclusive. It seems equally certain, however, that none of the experiments has been on a

sufficiently extensive scale to carry complete conviction on the point. . . . Taken together, they provide a quite considerable amount of the ever-growing body of circumstantial evidence for the theory.'

A striking case among the few others in which a real adaptation into a new environment seems debatable is the experiment of Dallinger.[78] This American student worked with three species of Flagellata which first showed an upper temperature limit of 23° C. When the temperature approached the upper limit, heavy vacuolization of the protoplasm occurred, preceding death. But when the culture was kept at 21° C. for 1–3 months, it could be shifted to 23° C., then after the same interval to 25° C., and so on, until, after 7 years, the species lived at 70° C., a temperature not endured by any animal in nature. The experiment broke down due to disorder in the thermostat. Only two possibilities may offer an explanation. The sojourn within the high temperature may induce a physiological reconstruction of the organism which induces the shift of its upper heat tolerance. Cases of such reconstructions are well known and the case of *Aurelia aurita* from Nova Scotia and from Florida may be quoted.[79] But the orthodox geneticist denies such possibility, believing that the heat induces many mutations, some of which show a higher heat tolerance than the type population. What occurs after the shift of temperature is negative selection, only the new mutations fitting into the changed environment being able to survive. Such cases in which previous chance mutations enable the organism (but not its original population) to enter a new environment are called pre-adaptations.[80] This controversy between real adaptation and pre-adaptation regularly reoccurs in any case of pretended adaptation, and it is most unfortunate that no *experimentum crucis* has yet been discovered to decide between either proposed solutions. The answer does not need to be an alternative one, but possibly, or even probably, both cases are realized in nature. Environmental conditions often induce a physiological or morphological reconstruction of the organism. These are active responses of the animal to external stimuli and no mere physical responses to physical actions. Those reconstructions are either at first phenotypical, and may become later on Dauermodifications, or they are based on mutations (pre-adaptations). All these responses of the organism are primarily without any relation to utility, being merely responses to stimuli. In some cases, as in those of the adaptation of animals to the local climatic cycle, in the white colouring of polar animals, in the surface decrease of larger animals in colder climates, &c., the animal decidedly benefits from those responses. In many or perhaps even most cases no benefit at all is recognizable. In no case does this response surpass the hereditary base of reactions, and therefore no real adaptation to a new environment ever occurs. What is called adaptation is really a response to environmental stimuli within the hereditary reaction base of the species, but without preconsideration of the utility of the response towards the changed environment. Whenever only the responses fitting well into the new environment are understood as adaptations, this should be especially stated. The term 'inaptations' is proposed for them.

We believe that Dauermodifications as well as pre-adaptations, perhaps even pre-inductions (in Woltereck's[81] sense), govern the changes in form, function, and behaviour of organism in varying environments. In no case is the reaction a simple physical one. The organism responds to the environment on its own. The fact that the organism and its way of response are the real point of interest has often been forgotten by those who measured the environmental factors as well as by those who counted only genes, chromosomes, and single characters.

## 7. OUTLOOK

Every biologist admires the great achievements of modern genetics and respects the strict methods of genetical thought, the logic of its morphological and experimental basis. But the undisturbed peace of mind of the geneticist is not a final aim of biological research. The fact that no morphological or physiological basis for environmental hereditary-induction, for heredity of morphological, physiological, or behaviouristic reconstructions resulting as reactions of the organism to enforced environmental conditions is known, and that no bridge has as yet been discovered for the morphological understanding of the parallelism between phenotypical and hereditary geographical variation under the influence of the same factor, does not justify the rejection of such possibilities. That in some of these problems cytoplasmic influence counterbalancing the gene-chromosome mechanism may be made responsible has by now been realized at least by some outstanding geneticists.[62] As long as such important branches of biology as ecology, zoogeography, comparative anatomy, palaeontology, taxonomy, and experimental morphology are forced to declare that, following their own methods, some kind of Lamarckian theory 'is probably the only intelligible theory of a natural evolutionary process ever advanced',[82] it is the duty of the geneticist to reconsider the actual limitations of his present methods and to help his fellow scientists to understand those problems in which we all are equally interested. At no time has co-operation seemed more necessary between all those scientists who are interested in the understanding of the living organism and the interactions of all intrinsic as well as extrinsic factors influencing it. To modern genetics we owe the abolition of that type of thinking with the aid of which understanding of the living organism was looked for by theories based entirely on deductions from insufficient facts alone. Modern ecology is trying to gather reliable facts into a comprehensive whole. Co-operation is most urgently needed for the interpretation of these facts as well as of those gathered by genetics (in the broadest sense, including development mechanics, &c.). And we doubt whether any one side will be able to understand the living organism by means of its own methods on its own right alone.

It would be to misunderstand the intention of the author if this essay were taken as supporting the Lamarckian theory. But a plea is made for a fully unprejudiced approach to the problem, as opposed to the *a priori* orthodox attitude of a large majority of present-day biologists.

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# NOTES

(*a*) p. 2. The exception of twins from one egg, as is the case in identical twins in man or in the polyembryonic offspring of *Tatusia* and certain parasitic Hymenoptera, is obvious.

(*b*) p. 58. This may be regarded as proof that under the conditions of this breeding the surface area of the agar was of importance, being the only factor equal in all three series. The duration of the total culture was longer in series 3, where the agar was higher and dried out later than in the series 1 and 2.

(*c*) p. 62. Dead flies: first column: actual ciphers; second column: smoothed ciphers to be applied in the last column (Total).

(*d*) p. 64. The columns below 'living' indicate the total number of all living stages of the *Drosophila*-population, in case the adult longevity is assumed to be 13 days invariably or lasting 2–13 days according to the empirical experience of our breedings.

(*e*) p. 72 and 73. Until the first appearance of the new generation the ratio is equal: 4 × 12:5 therefore appears instead of 4 × 15 eggs.

(*f*) p. 80. Only after the manuscript was ready for publication, a very comprehensive experimental paper on *Drosophila*-populations appeared by Ph. L'Heritier (*Arch. Zool. Exper.* **78**, 1937, p. 255). Aims and technique are quite different from those of our study. Both papers are complementary, and the attention of the reader interested in animal populations is turned to it.

(*g*) p. 100. Another and perhaps even better indicator for the raised vitality in North America as compared with Europe is the fertility: Zwoelfer (1927, 1929) reports 240 eggs from south Germany, all American authors (as Huber, 1928, Caffrey, 1927, Vinel, 1919), about 400 eggs per female.

(*h*) p. 162. In Ciliata the effect of the Dauermodification disappears in some cases following the first copulation. After this act the plasmatic influence is subdued by the nuclear, or better, by the chromosomal conservative mechanism. This is confirmed by crossing with the original strain, where maternal influence only preserves the modification (cytoplasmatically). In other cases the modification is still recognizable even after half a year, after many copulations.

# INDEX

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